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# ON THE APPLICABILITY OF AGENT BASED MODELLING IN BEHAVIOURAL ECOLOGY

Submitted by Hagen Lehmann  
for the degree of  
Doctor of Philosophy  
of the University of Bath  
2009

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# Abstract

This dissertation contributes to different interdisciplinary research fields. It examines different theories about the reasons for the evolution of social structure in gregarious animals and the role of social dominance in this process and uses agent based modelling (hereafter ABM) as relatively new technique to test the coherence of different theories from behavioural ecology.

ABM is a computer simulation method for testing the collective effects of individual action selection. With ABM it is possible to build agents with individual characteristics and then monitor the effect individual behaviour has on a group level. This dissertation focuses on the introduction of ABM as technological tool into behavioural ecology. It discusses the potentials and limits of the usage of agent based models in this field by reviewing the epistemological background of modelling in the scientific process. This dissertation gives examples of the ABM process by critiquing one of the already established agent based models in primatology and by introducing a set of new models.

The model criticised is DomWorld. Its successful replication exposed problems with the ecological validity of different factors it is based on. By successfully testing the consistency of one of the theories dominating the field of social ecology additional evidence for the validity of this theory is provided. With a new set of models the effects of different variables on the evolution of social dominance and social hierarchy are tested. These successful applications and the discussion of the epistemological background of ABM provide a basis for further implementations of agent based models and research in the area of behavioural ecology.



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## Related Publications

The following list includes all papers published by the author which are related to this dissertation.

**Lehmann et al. (2005) Tolerance and Sexual Attraction in Despotic Societies: A Replication and Analysis of Hemelrijk (2002)** Hagen Lehmann, J. J. Wang and Joanna J. Bryson, Proceedings of the Symposium on modeling natural action selection. 2005, Edinburgh, UK

**Bryson et al. (2007) Agent-based models as scientific methodology: A case study analysing primate social behaviour** Joanna J. Bryson, Ando Yasushi and Hagen Lehmann, Philosophical Transactions of the Royal Society, B — Biology. September 2007, Volume 362, Number 1485

**Bryson and Lehmann (2009) Selection for Variation: Evolutionary Processes Affecting Dominance, Social Structure, and Female Mate Choice** Joanna J. Bryson and Hagen Lehmann. Poster at European Human Behaviour & Evolution Association Conference, 2009





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# Chapter 1

## Introduction

### 1.1 Agent-based models in social science and behavioural research

One of the main philosophical questions in science is how do we know what is true and what do we consider as knowledge. In life sciences in general what we consider as truth is mainly based on what is observed in experimental and in natural settings. With the advancements of computer technology a third way of testing our hypotheses and accumulating knowledge has become more and more influential (Ostrom, 1988), the application of agent based models. Computer technology enables researchers of all scientific fields to generate artificial environments in which interaction effects of different hypotheses of complex theories can be tested. With agent based models it is possible to generate even more controlled environments than in normal experiments. They can help us to understand existing theories in testing their consistency.

There have been different attempts to implement agent based models into behavioural biology. Even though the use of computer simulations in behavioural research is increasing, the field is still sceptical about their appropriate application. Due to its structure, the relatively new field of agent based modelling (hereafter ABM) represents a technology which could prove very helpful to behavioural research. The interaction dynamics of social agents like members of

primate groups emerge usually due to an interaction between environmental conditions and internal traits of the agents involved in these interactions. The complexity of such settings makes it hard to understand these dynamics and to make valid predictions based only on observation. Agent based models enable us to model agents with individual traits in dynamic environments. This makes them especially useful in behavioural research dealing with small social groups (Macy and Willer, 2002). Nevertheless the generality of their results and their ecological validity are still discussed controversially. One of the aims of this work is to show the potentials and restrictions for the use of agent based models in this area of science.

## 1.2 Social structure in primates

In order to understand the nature of our own social structures humans have always looked at the different types of social organisations found in the animal kingdom. Especially the social structure of primates has been in the focus of anthropological behavioural researchers in the last century. The questions “why do animals live in groups” and “how did the variety of social organisations found in different primate species today evolve” have been answered gradually and more and more accurately with increasing knowledge about different species.

Comparative behavioural research on different species of non-human primates started around 50 years ago. With the accumulation of knowledge about the inter-individual interaction patterns of different non-human primate species the differences and similarities in behaviour between these species became more and more obvious. The resulting question was “what are the reasons for these differences?”. In order to find an answer it was at first necessary to explain the reasons for the existence of social groups. Hamilton (1971) proposes predation to be the reason for the evolution of gregarious lifestyle. Following his theory, animals live together because the group provides protection from predators.

One of the consequences of group living are different forms of social styles. Social style can be defined in different ways. One of the definitions is as variety of behaviours an individual exhibits while interacting with other members of its own species. In other words how many distinguishable different action patterns

an individual uses in a social context. This includes, besides how frequently and intensely a behaviour is executed, also how large the behavioural repertoire of an individual is. In primates the distinction between different social styles is based on the dominance style of the different primate species (Hand, 1986). The dominance style is defined as the gradient of hierarchy (van Schaik, 1989). The steeper the group hierarchy of a species is, the more despotic the species. For example Thierry (2004) postulated that different macaque species have different social styles based on their inter-individual tolerance levels and classified these social styles according to different behavioural characteristics into four grades ranging from despotic to egalitarian.

The *phylogenetic inertia theory* (Thierry, 2006) focuses on the genetic heritage of a species, the migration patterns and on archaeological evidence. It postulates that the social style of a species is relatively stable and changes only little over time. It also suggests, based on the current distribution of different macaque species with different different social styles, that the more egalitarian interaction patterns are older than more despotic ones. In the theory the existence of differences in the social structures of the species is explained mainly with genetic drift. The *socio-ecological theory* (van Schaik, 1989) postulates that for most non-human primate species environmental changes have a critical impact on their social behaviour and changes in the environment change the way individuals in these species interacted with each other.

Hemelrijk's theory (Hemelrijk, 1999b, 2000, 2002a) includes statements of the phylogenetic inertia theory. Her theory deals with reasons for the transition from one social structure to another and with male female dominance interaction. Hemelrijk assumes, like the phylogenetic inertia theory, that the egalitarian social structure preceded the despotic structure. This assumption is based on the findings of e.g. Matsumura (1999) and Thierry (2000). According to Hemelrijk primate males are usually dominant over females, due to their bigger size, strength and higher level of aggression, but females can nevertheless outrank them in their periods of receptiveness due to an increased interaction frequency (Hemelrijk, 2002a). Hemelrijk constructed a model called *DomWorld* in order to test her assumptions. The detailed description and explanation of *DomWorld* is the subject of chapter 5.

Other factors like matrilineal dominance inheritance and female mate choice are



also considered to have an influence on the evolution of social dominance (Manson, 1994a). In some primate species females inherit their dominance rank in the hierarchy from their mothers (Silk, 2007). For females, their lifetime fitness depends on their dominance position in the group. High ranking females have higher lifetime fitness than low ranking females (Silk, 2002, 1993). Therefore any reproductive advantages dominant females accumulate will be magnified over time due to the inherited stable dominance ranks (Silk, 2007).

Each of the above introduced theories was examined and modelled. The *socio-ecological theory* was compared with the *phylogenetic inertia theory*. The results of these tests and comparisons can be found in section 1.4.

### 1.3 Definition of research issues

This thesis has two different research questions.

1. How can agent based models as technological tools help behavioural researchers find answers in the field of social evolution? What are the potentials and what are the restriction of such models?
2. Is it possible to test the consistency of the different existing theories about how environmental pressures influence the evolution of social dominance and social structure with working agent based models?

In order to answer the first question, different agent based models were implemented and tested and their results were discussed and compared against the background of existing theories in the field of primate social evolution. The function of models in general in scientific research is at the end of this work reviewed from an epistemological perspective in order to illustrate the usefulness and distinctive characteristics of agent based models.

Different theories and findings from empirical research were implemented into different versions of agent based models in order to answer the second question. The results of these implementations give additional insights on the phenom-

ena described and represent an abstraction and parsimonious explanation of the dynamics behind some of these phenomena.

In the course of answering the second research question different instances of agent based models were implemented. The code was made publicly available, providing a platform for discussion.

## 1.4 Contributions

One contribution of this work is the replication of Hemelrijk's *DomWorld* modelling environment (Hemelrijk, 2002a). Critical points in the implementation of different variables were found, discussed and suggestions about possible improvements have been made. This work should provide the basis for a better understanding of how to use ABM in behavioural science and what the problems of its use are. Parts of the model were extended and used in the other models discussed in this work. The code of the replication is available online for public discussion and has already spawned various critical comments and further replications.

Another contribution is the construction of a new set of models which aim at a better understanding of the dynamics of social evolution. The first of these models is an implementation of Hamilton's theory about group formation (Hamilton, 1971). The model is based on spatial distribution and hereditary transmission of social dominance. Since its results match the predictions derived from the theory it is based on, the model can be seen as successful implementation. The results suggest as predicted by the theory that social dominance, based on the ability to displace conspecifics, can be adaptive in the field of tension between the environmental variables predation and food availability. This model is called *Dominance Inheritance Model*.

The second model tests the effect of these environmental factors on two primate populations with different social structures living in the same environment. The difference between the populations are based on the phylogenetic inertia theory (Thierry, 2000) and the socio-ecological theory (van Schaik, 1989). It tests the coherency of the socio-ecological theory by comparing the results of the perform-

ance the two populations in different modelled environmental conditions with the findings and predictions of the theory. The results of the model largely fit these predictions and findings from empirical research and it can therefore be seen as successful implementation of the theory. Based on the results of the model and in the process of looking into the phylogenetic inertia theory and the socio-ecological theory and implementing one of them it became more clear that both deal with the same phenomena but use different definitions for the spatial distributions of the observed animals. Clarifying this misunderstanding between the two theories might further improve our understanding of the role the environment plays in the evolution of social structure and dominance. The phylogenetic inertia theory and the socio-ecological theory are seen as opposing theories, but by providing an explanation for the primary discrepancy between them, different definitions of spatial distribution, they have been unified in this dissertation.

The last new model represents an extension of the *Dominance Inheritance Model* and aims at modelling the effects of different social variables on the evolution of social dominance. In the model these variables are female mate choice, variance in male quality and rank fights. The results of the model correspond with different observations and predictions about the interaction of the tested selective factors with social dominance. By integrating the variables one after another into the model while maintaining the general structure of a model it is possible to test a variety of different theories on a similar topic. This illustrates one of the advantages of ABM.

While implementing different instances of agent based models based on theories from primatology and behavioural ecology this thesis analyses the strengths and weaknesses of agent based models in the field of behavioural research. This effort to improve ABM as technology and make it easier to use for researchers in different fields dealing with social phenomena is another contribution of this dissertation. The aim of systematically describing the process of development and implementation and providing information about the platforms used for it and also of publicly providing the developed code was to help this process.

The controversy about the use of agent based models in social science is mainly based on a misunderstanding of what such a model can and cannot do and on a lack of transparency in the implementation process of currently existing models. In a short philosophical overview of the functions of models in science in general

and agent based models in particular at the end of this work some of the misconceptions are clarified and a prospect for the future use of agent based models in science is given.

## 1.5 Structure of the thesis

The thesis is composed of four parts. In the first part the relevant literature from primatology and ABM is reviewed. The literature review from primatology is structured into two parts. First a detailed overview about the general theories of social evolution is given and the explanatory approaches for the reasons of gregarious lifestyle in many animal species are illustrated. In a next step an overview of the relevant data from primatology is given and the *phylogenetic theory* and the *socio-ecological theory* are described in detail.

After the review of relevant primate literature the ABM technology is described. Its basic principles are elucidated as well as its history in the field of social science. It is illustrated when and why to use agent based models in the scientific process and ABM is compared to equation based modelling, an approach for example used in testing effects of population dynamics. Also a description of the environment used to program the models in this thesis is given.

The second part of the thesis deals with the analysis and replication of *DomWorld*. Hemelrijk (Hemelrijk, 1999a, 2003, 2000) tested with this modelling environment different theories which dealt with the effects of female-male interaction patterns. In this work the structure of her modelling environment is critically analysed. Due to the lack of publicly available code the replication of her model was constructed based on information from some of her papers. Several experiments described by Hemelrijk (Hemelrijk, 1999b, 2002a) were conducted in order to test the accuracy of the implementation. Following this process problems and advantages of her model were analysed and critically discussed. The results of this analysis have been published (Bryson et al., 2007) and are directly referenced in other articles.

The third part of the dissertation presents and analyses a new set of models. Based on the replication of Hemelrijk's model, which dealt with social dominance between males and females, a set of new models is introduced. The first

model approaches the question of possible reasons for the evolution of social dominance in general. The second model is an implementation of the socio-ecological theory, which tries to give an answer to why there are different social structures in different primate species. It tests the consistency of this theory and attempts to reconcile it with the phylogenetic inertia theory, which is its primary opposing theory. Several sets of experiments are run within the modelling environment and the results of these experiments are presented. The third model is an extension of the first and tests the effects of other hypothesised social and environmental selective pressures on the evolution of social dominance.

The final part of the thesis presents the conclusions and analyses the contributions of this work. It discusses the use and possible future role ABM could play in behavioural science based on the results of this thesis and from an epistemological perspective.

# Chapter 2

## The evolution of social behaviour

### 2.1 Introduction

One aim of this research, besides testing the usability of agent based models in behavioural social science, is to test the coherence of different theories about the reasons for the existence of different social structures in primate societies. With increasing data and more complete observation of almost all primate species on the planet, a comparative approach to the problem has been adapted by socio-ecologists working with primates. The large database has enabled social scientists to postulate a variety of different theories about social evolution.

#### 2.1.1 Initial questions

In order to get an overview of the problem it is at first necessary to examine the key questions concerning the topic:

1. Is predation one of the starting points of the evolution of social structure, the way Hamilton (1971) describes it?
2. If this is the case, why does a gregarious lifestyle exist in habitats without predation? What could be other reasons for animals to live in groups?

3. What is the qualitative difference between a social group and an aggregation?
4. What is the nature of social coherency and what environmental conditions are the constraints for its existence?
5. Is social dominance a necessary precondition of social coherence or is it a result of a gregarious lifestyle?
6. Does gregarious lifestyle necessarily result in an evolution of dominance or group hierarchies?
7. What are the environmental constraints making dominance beneficial to the individual or group? What costs for the individual or the group does dominance have?
8. Why do different types of group hierarchy or social structures exist? What social structures have evolved under what conditions?
9. To what extent does dominance behaviour within a group determine the kind of social structure the group has?

The first five of these questions refer to the nature of grouping as basic structure of socialisation within a species. These questions will be answered in the first part of this chapter. The role of predation in the process of group formation will be explained as well as the function of social dominance and vigilance as possible reasons for the formation and maintenance of social groups.

The other four questions deal with the modality of an already evolved social structure. The reason for the evolution of different forms of social structures are the framework of the theoretical social science background of this dissertation.

By covering these background theories this chapter hopes to provide the necessary information to better understand the theories about the explicit nature of different social structure which will be introduced in chapter 3.

## 2.2 Factors effecting grouping — An overview

Animals can live a solitary lifestyle or they can live in groups. The specific social structure in which individuals live together is the result of an environmental adaptation process. This adaptation can be understood as optimisation process in which fitness is maximised on an individual level. Group living is for the individual connected both with advantages and disadvantages. The competition within a group for mating partners, food and other resources can outweigh the advantages, like the protection from predation, an individual gains by living in a group. The bigger the group the individual lives in is, the bigger are the disadvantages which act as selective pressures on the individual (Waser, 1977; van Schaik et al., 1983; Janson and van Schaik, 1988; Isbell, 1991; Olupot et al., 1994; Krause and Ruxton, 2002). From this perspective the grouping process is another selective factor for the individuals in the group, according to which they adapt their behaviour. The social structure of a group develops and changes over time during this adaptation process.

The social structure in which individuals live in is therefore the result of two factors. The first factor (the *ecological* factor) includes all the environmental conditions an individual is confronted with and from which the grouping process as one form of adaptation results. The second factor (the *social* factor) describes how the individuals adapt to the emerged group structure. The way the gregariousness of the individuals is specifically organised is in turn a result of the interactions between these two factors.

The development of specific social structures is a dynamic process. Otherwise every specific form of social structure would match the specific set of environmental conditions in which it would increase the fitness of the individuals most efficiently.

This following sections of chapter 2 deal with the first factor, with the environmental conditions which influence the process of grouping. Here three main influential factors can be defined: access to resources (Krebs and Davies, 1993), predation pressure (Dunbar, 1988; Hill and Dunbar, 1998) and cooperation possibilities (Emlen, 1991; Dugatkin, 1997).

Concerning the ecological factor of access to resources the resource dispersion



hypothesis (hereafter RDH) (Carr and Macdonald, 1986) was very influential. The RDH includes three hypotheses (Carr and Macdonald, 1986; Macdonald and Carr, 1989; Bacon, 1991; Blackwell, 2001; Johnson et al., 2001):

1. The size of a group is not correlated with size of the environment it lives in.
2. The size of a group is correlated with the heterogeneity/homogeneity of the available resources regarding their spacial distribution and occurrence in time.
3. The size of a group is correlated with the richness of the available resources.

These correlations are to be seen relative to the body size of an individual of a species (Swihart et al., 1997). According to the RDH it would be for instance possible to conclude that polar bears have a solitary lifestyle (Ovsyanikov, 1996) because their calorie demands and spatial needs are high compared with the food density in the habitat they live in. On the other hand it would also be possible to argue based on the RDH that orangutans live more solitary lives (MacKinnon, 1974; Rodman, 1979) because food is everywhere available in their environment and because originally there was enough space for a for such a lifestyle. These examples illustrate one of the main points of criticism concerning the RDH. It is not falsifiable. It is possible to interpret every empirical result in such a way, that it fits the RDH (von Schantz, 1984). But for the discussion in this chapter it is only necessary to keep in mind, that the RDH makes predictions about the relationship of group size, type of food and food distribution, but does not give direct causal predictions about the reasons for group formation in the first place. Taking the criticism of the RDH into consideration, it seems to be problematic to assume that food quality and distribution are a sufficient enough reason for the evolution of gregariousness.

Wrangham (1980) suggests based on empirical evidence that predation could be an adequate reason for the evolution of grouping. Living in social structures provides safety from predation and is therefore advantageous for the individual. An increase of group size is correlated with an increase of the overall vigilance in the group (de Ruiter, 1986; Isbell and Young, 1993). Nevertheless it is hard to differentiate whether the protection from predation is the primary reason for the

evolution of group living or whether it is one of its consequences. Bigger aggregations of individual animals enable always more effective protection strategies for the entire group than the life in smaller groups or as solitary individual. In groups it is for example possible to develop certain protective behaviour patterns like a cooperative attack on the predator (Boesch, 1991), which are not observed in solitary individuals. It is also necessary to bear in mind that predation as selective pressure is not constant, but changes depending on the group size of the prey (Endler, 1986).

Even if individuals in larger groups can reduce their risk of being killed by predation (Rodman, 1988; van Schaik, 1983; Crockett and Janson, 1993), this by itself is not sufficient to predict a causal relationship between a high predation rate and a more gregarious lifestyle of the prey. The problems with proving such causal relationships are on one hand based on the fact that it is hard if not impossible to design experimental studies over evolutionary relevant periods of time. On the other hand it is difficult to evaluate correct predation rates in the wild, because in the majority of the cases they are relatively small and include a high variance. Cheney and Wrangham (1987) estimates the median of the annual predation rate of 24 primate species with only 3% – but with a range from 0 to 15%. Most of the predation events happen during the night, which makes it difficult to observe them (Goodman et al., 1991; Busse, 1980) and they seem to be less frequently if the predators sense the presence of human observers (Isbell and Young, 1993). In consequence it could be possible that the variance of the actual observation error is higher than the differences in the empirically observed predation rates. Taking this in consideration it seems to be less clear whether predation can be seen as the reason for the evolution of gregariousness – even if living in groups has a selective advantage for the individuals due to the protection from predation.

Predation pressure on for example primates decreases with increasing body size of the primates. A re-analysis of a study by Clutton-Brock and Harvey (1977) showed that the body size correlated not only with the predation rate, but in interaction with the group size predicted the predation rate more accurate (Cheney and Wrangham, 1987). A bigger body size is also correlated to a higher food demand and group size is negatively correlated to individual foraging success (van Schaik et al., 1983; Janson and van Schaik, 1988). On one hand the group offers better protection from predation to the individual, allowing it to spend more time on foraging. On the other hand the competition for available food resources

increases with an increasing group size.

van Schaik et al. (1983) postulated that predation and food availability and its distribution are together the decisive selective factors for the evolution of gregariousness. Predation pressure being the more decisive selection mechanism for group size and birth rate is modulated by the type of available food and the way it is distributed.

Fundamentally are all of these theories based on the basic theory of Hamilton (1971) about group formation. This theory, cooperation between individuals as possible selective factor for group formation and the difference between a social group and an aggregation of individuals will be discussed in the next sections.

## 2.3 The influence of predation

Systematic research about what could have caused the evolution of a social groups in animals was initiated with Hamilton's theory about the reasons for gregarious lifestyle (Hamilton, 1971). In his work Hamilton postulates predation to be the main environmental pressure forcing animals to live in groups. According to him an individual which in case of danger prefers to stay in close proximity of its conspecifics reduces its own risk of being eaten by increasing the risk of the group members next to it.

In a thought experiment he uses frogs sitting around a circular pond with a snake living in it and hunting the frogs to illustrate his point. If a frog sits at the pond by itself its risk of getting killed is relatively high. If the snake looks for prey in its direction it will only find this one frog. But if there are many frog in the same direction close to each other the chance for each single frog to get killed is reduced. If the goal of each frog would be to reduce its risk of getting killed by the snake, each of the frogs would try to reduce the risky space around it by jumping over the frog next to it. The result would be that in an extreme case the frogs would pile up in one spot on the side of the pond (Hamilton, 1971).

This of course is a very simplified explanation of the problem. Hamilton uses in a second step lions and cattle in open territory. By showing the geometrical

possibilities and constraints for the cattle to move into closer proximity of each other or staying close together he can show that this type of grouping behaviour is in case of an immediate threat very advantageous for the animal executing it and increases the reproductive fitness of the animal immediately. According to him it is therefore very likely that this type of behaviour was selected for on an individual level. Even more so since it is easier for the grouping individual to seek shelter close to its conspecifics if all the other members of its group aren't moving.

Grouping behaviour can be found across taxa being most prominent in schooling fish, large herbivores like wildebeests or flocking birds. Hamilton gives a variety of examples from different species and studies in order to support his theory (Crook, 1960; Darling, 1937; Lorenz, 1966; Tinbergen, 1951).

## 2.4 Gregariousness without predation

The most obvious question arising from Hamilton's theory is: why do animals live in groups in habitats without predation? For most of the big solitary living predators like bears, tigers or leopards this is the case. But there are other predators like wolves or hyenas which live in groups and are also not preyed upon. There must therefore be other reasons besides predation which lead to gregariousness.

This seems to contradict Hamilton's theory, but there are at least two possibilities to explain this incoherence between theory and observation. On one hand hunting in groups itself could have been an adaptation to grouping tendencies in the species the predator preys on. Sometimes it is more efficient to hunt group-living animals in packs than in a solitary fashion. From this perspective group-living in predatory species could have been an adaptation to the adaptation of the prey species to live in groups. On the other hand group hunting could have evolved since it enables predators to kill animals far bigger than them. Wolf packs in Canada pose a serious threat even on adult moose, a prey a single wolf would stand no chance against (Hayes et al., 2000).

Another reason for gregarious lifestyle in animals which are not exposed to predators during their adulthood is offspring protection. Female lions keep their

newborn cubs in solitary dens for several weeks before bringing them to communal dens with other females (Packer et al., 2001) in order to reduce the risk of infanticide by males strange to the group. At least in mammalian species males can increase their reproductive success by shortening the weaning period of the females and in this way make them receptive quicker after they gave birth.

Infanticide behaviour is also observed to various primates species (Cheney et al., 1988; Collins et al., 1984; Watts, 1990). Its role has been discussed from the perspective of female social behaviour (van Schaik, 1989) and female-male social relationships (van Schaik and Kappeler, 1997). Infanticide risk leads to closer association between different individuals in a group and therefore promotes group formation. Males sometimes aid females by protecting their offspring from infanticide by other males (infanticide-avoidance hypothesis (van Schaik and Dunbar, 1990)) or via paternal care (Kleinman, 1977).

These examples illustrate that the formation of groups can occur in species which are not exposed to predation or which are not preying on other group living animals. It is therefore likely that predation is not the only factor responsible for the evolution of gregariousness. It seems that beside predation, the advantages provided by different forms of cooperation between individuals also have an influence on this process. Nevertheless the goal of this thesis and the models presented in its course is to examine the influence of ecological factors like predation and food availability on the process of group formation. Examining the influence of cooperation is therefore not an immediate goal of this work, but it is necessary to mention it as a potential factor in the evolution of gregariousness.

## 2.5 Vigilance

One benefit of group living is that it results in a lower necessity for vigilance behaviour for each individual in the group because the probability of spotting a predator is higher if more “eyes” are watching. An individual has therefore a safer position within a group than as a solitary animal. This implies a reduction in individual vigilance with an increase in group size (Barnard and Thompson, 1985; Quenette, 1990). The functional interpretation of this reduction is still poorly understood. There are two main hypotheses explaining the existence of

an inverse relationship between group size and vigilance, called “group size effect” (Lima, 1995).

The first hypothesis states that animals benefit from grouping because the vigilance of many individuals leads to an increase in the probability of detecting a predator within the time it needs to attack (Pulliam, 1973) and that individuals in larger groups can enjoy the same or an improved predator detection rate while scanning less frequently and having more time to feed (Pulliam, 1973). In detail Pulliam’s model describes the probability of at least one member of a group detecting a predator in terms of individual vigilance rates, group size and predator approach time. Given a constant level of group or “corporate” vigilance, individual vigilance levels can be decreased by increasing group size. This is called the “many eyes effect” (Powell, 1974), the “collective detection effect” (Lima, 1995) or the “detection effect” (Dehn, 1990).

The other hypothesis states that if vigilance depends on predation risk and if that risk declines with increasing group size, vigilance should also decline with increasing group size. The possibility of such an effect has been considered by many (Bertram, 1978; Pulliam et al., 1982; Packer and Abrams, 1990; McNamara and Houston, 1992). But it is not clear whether predator detecting is the only function of vigilance. In fact vigilance may have a number of functions in obtaining information about the environment (Lima, 1990), like the location of other food sources or groups of individuals of the same species.

Vigilance could therefore be one of the factors linking predation risk and grouping, because less time spent on predator detection means for the individual more time is available for feeding, sleeping or mating. In any case, there is an observed correlation between vigilance and the risk of predation (Roberts, 1996; Frid, 1997). But this correlation does not imply causality. All studies, compared in the review of Elgar (1989) found a reduction in individual vigilance with increasing group size. He concludes that most studies fail to demonstrate a real unambiguous relationship between predation risk, vigilance behaviour and group size. A reduction in vigilance of the individuals with increasing group size could also arise if group size relates to some other factors which in turn affect vigilance. For example, larger groups may tend to feed on better food supplies and animals feeding on better food supplies may spend less time on other activities such as vigilance.

This leaves the possibility that increased group size does not provide a better detection of predators but only reduces the pressure to be vigilant. This in turn means the effect of grouping may still be induced by predation, but the effect of increasing the group size may not be the direct result of predation. An increase in group size by itself does not automatically provide a better detection of predators. Therefore the question to be answered is, what are the causes and what are the results in the process of evolution of gregarious lifestyle? In order to find an answer at first it is necessary to examine under what circumstances does group size change?

Different studies investigated the effects of group density on vigilance (Lazarus, 1978; Holmes, 1984; Roberts, 1988). All found an increase in vigilance to be correlated with an increase in neighbour distance. Pöysä (1993) found that group size did not relate to vigilance when neighbour distance was controlled for, whereas neighbour distance had an effect on vigilance after controlling for group size. Bednekoff and Lima (1998) showed that the correlation between the detection of predators and the predation risk dilution for the individual strongly depends on the way how the information about the predatory attacks is shared in the group. If the information is only partly transmitted, which is mostly the case in the wild, the size of beneficial effects of gregariousness for the individuals in the group decreases (Bednekoff and Lima, 1998).

In summary it can be said that the correlations between vigilance, gregariousness and predation protection behaviour are still not fully understood. The advantages shared vigilance in groups has for the individuals strongly depend on the cooperative behaviour exhibited between these individuals and on the way information is shared. There are no doubt beneficial effects in shared vigilance, but they depend on complex interaction patterns and are therefore most likely a result of more basic mechanisms of grouping behaviour. As mentioned before the goal of this work is to understand these more basic mechanisms. Nevertheless it is important to mention the more complex social behaviours at this point in the thesis in order to understand the motivation for the models presented later on.

## 2.6 The difference between social groups and aggregation of animals

From mere observation it can be difficult to discriminate a social group from an aggregation of animals of the same species, especially in a feeding situation. So what exactly are the qualitative parameters which differentiate a social group from an aggregation of animals? Since a social group remains as a group even in situations without predation or feeding there is probably an additional cohesive force besides more efficient feeding possibilities or immediate predation pressure to hold the group together.

As discussed in section 2.2 predation pressure and resource restriction were very likely the crucial constraints which lead to the evolution of gregariousness. But complex grouping behaviour seems to be expressed even in the absence of these two proximate stimuli. Therefore during the evolution of gregarious lifestyle a propensity for group structure must have evolved. This characteristic is called social coherence (Alexander, 1974). It is the reason why groups seem to stay together independently from the current constraints of the environment.

As described in Hamilton (1971), individuals in groups are more successful in predation avoidance than solitary individuals, but competition in the sharing of resources and of living space in the centre of the group are the main disadvantages of group living. The group structure resulting from Hamilton's theory is a mere agglomeration of individuals in a small space in which these individuals stay in close proximity to one another. His theory does not imply that there is or is not a structure in such a group. It only states that animals need to be in proximity to each other, but not how this is achieved. This tendency to "herd" is by itself only one of a variety of adaptive behaviours to avoid harmful situations for an organism. From this point of view "herding" represents in a way "anticipated" readiness to escape. Anticipated because groups (herds) exist without an immediate danger or presence of a predator.

Alexander (1974) published a theory, in which he claims that the difference between the costs of cooperation and competition for each individual in the group determine the degree of cohesion of the group. If the common costs of a solitary lifestyle are much higher than the cost of competition within a group, then



gregarious lifestyle evolves in a population. He also argues, that if subordinate members of the group have for example the option to leave, this option limits the power of the dominant (Alexander, 1974). By arguing this way Alexander (1974) assumes that gregarious lifestyle is connected to dominance hierarchies.

This leads two questions:

1. Does the formation of groups (as an adaptation to predation) tend to result in an evolution of dominance or group hierarchies?
2. Is dominance a necessary precondition of social coherence?

## **2.7 The evolution of social structure — dominance behaviour**

A first characteristic to differentiate an aggregation of animals from a social group is the concept of social coherence. Social coherence describes the independence of interaction patterns that individuals in a group use to engage socially with each other, from the circumstances these interaction patterns have evolved in.

Most of the interactions between group members are beneficial responses like grooming. “Strangers” on the other hand are often attacked or repelled. Research on domestic fowl shows that when strange hens are introduced into flocks they immediately become the target of aggression (Schjelderup-Ebbe, 1935; Guhl and Allee, 1944). This might be evidence that there is a causal relationship between social coherence and aggressive behaviour (against out-group individuals). This relationship may be constitutive for the evolution of social groups but not for the aggregation of animals.

The capability to differentiate in-group individuals from out-group individuals facilitates both the selection of aggressive behaviour and the social coherence of the group. In this context conflicts within the group have to be solved differently from conflicts with out-group individuals, because otherwise social groups would not differ from aggregations. Groups need to solve conflicts between their members in a more efficient way than via permanent agonistic struggles between

individuals. A group needs a social structure to be a social group, otherwise it would only be an aggregation of individuals. For different primate species different types of social structures have been defined (Thierry, 1994, 2004). These different types of social structure range from egalitarian to despotic. The differences between are mainly based on the way individuals behave towards each other during conflict situations. The more tolerant they are towards each others proximity, the more they are considered to be tolerant. This will be discussed in more detail in chapter 3.

It seems that in order to a better understand of the evolution of social structures is it necessary to better understand dominance behaviour, because social organisation seems to have developed to solve in-group conflicts more efficiently. Conflicts within a group are induced like any other conflict by two factors: the “object” the conflict is about (e.g. food, mate, space) and the motivation to fight based on the assessed probable outcome. This way the evolution of social structure is connected to the how an aggression potential within a group is diverted.

In the first scientific definition of dominance, Schjelderup-Ebbe (1922) describes the impact of dominance behaviour on social structures as follows:

“Dominance is an attribute of the pattern of repeated, agonistic interactions between two individuals, characterised by a consistent outcome in favour of the same dyad member and a default yielding response of its opponent rather than escalation. The status of the consistent winner is dominant and that of the loser subordinate. Dominance status refers to dyads while dominance rank, high or low, refers to the position in a hierarchy and, thus, depends on group composition.”

Based on this definition different attempts to operationalise dominance have been made in order to make the dominance and the rank of an individual calculative. A possible operationalisation of dominance is realised by Henderson and Hart (1995). They define the success of agonistic interactions by the quotient of how many confrontations an animal wins and how many it loses multiplied with the quotient of how many individuals were supplanted by an animal and how many individuals supplanted the animal. This equation takes both the proportion

of interactions won and the proportion of individual animals supplanted into account. Based on the success score ( $R$ ), a rank number is assigned to each animal. The rank is then scaled between 0 and 1 (most and least dominant male, respectively).

There are different explanations for the reason of the existence of social dominance. A very minimalist explanation was proposed by Hemelrijk (2000) and demonstrated in her *DomWorld* models. She assumes that social dominance serves only to reduce aggression without having an adaptive advantage and that the formation of dominance hierarchies is only a side effect of the interactions between the individuals of the group (Hemelrijk, 2002a).

On the other hand social dominance is associated with a higher overall fitness of the individuals of a species because it is supposed to enable individuals to have better access to resources like food, potential mates and central position in the group to protect them from predation. Social groups are usually structured in such a way that some individuals are consistently more successful in obtaining resources when there is a conflict than others (Allee, 1952; Drews, 1993). Because dominant individuals, in this definition of dominance, have access priority to resources, it is generally assumed that these individuals also attain the highest reproductive success. The nature of the advantage in fitness for socially dominant individuals is crucial for the understanding of the reason why dominance hierarchies exist.

If dominant individuals would not benefit from being dominant, their investment in acquiring and maintaining social dominance would be wasted (Pusey and Packer, 1997). Such investments are, for example, costly signals used in agonistic interactions (Zahavi and Zahavi, 1997), harmful side-effects of increased androgen levels (Folstad and Karter, 1992; Frank et al., 1995; Packer et al., 1995; Buchanan et al., 2001), or an increased risk of injury. These costs could potentially even outweigh the benefits of having access priority to resources, resulting in neutral or even negative effects of social dominance on fitness (Rohwer and Ewald, 1981; Ellis, 1995).

Various studies of primate behaviour have reported positive or at least neutral effects of dominance on reproductive success (reviewed in Ellis, 1995), providing support for the assumption that dominance is beneficial. But on the other hand

in captive animals negative effects of dominance on indicators of reproductive success have been found (Ellis, 1995). But even if dominance is not advantageous for the most dominant individual, maintaining a dominance hierarchy might be beneficial for the average individual or the entire group. It is possible that the most dominant individual is “pushed” into its position, because there are always losers in groups with a hierarchical structure. These arguments show that the relationship between dominance and reproductive success is still poorly understood.

Some think the group structure itself is the result of environmental constraints during the process of the evolution of gregariousness in a species (van Schaik, 1989). The main effect would be the adaptation of the spatial structure of a species to the environmental conditions it lives in. The question which has to be asked in this case is how long does this process take and how strong is the plasticity of its result. In other words, if a species moves after developing a gregarious lifestyle because of strong predation pressure in a habitat without predation, is it possible for this species to change its social structure? If yes, how long would this take and what would be the factors influencing this process?

## **2.8 The nature of socialisation: A top-down vs. bottom-up approach in behavioural research**

Socialisation is often explained by a top-down approach (Boake, 2002). From this perspective the process of socialisation depends on relatively sophisticated cognitive skills (Barton and Dunbar, 1997; Dunbar, 1996). Following this we have to localise which cognitive skills enable the social life between individuals. It is argued that animal societies exist because of implicit social contracts which allow some of the problems of survival and reproduction to be solved cooperatively. These contracts work because they allow problems to be solved more efficiently than with fighting (Dunbar, 2003; Cosmides and Tooby, 2005).

However, these social contracts require the individuals involved to be willing to forgo some of their more immediate personal interests in order to profit later from greater group-level cooperation benefits. If too many individuals of the group would act according to their own selfish interests, the cohesion of the

group would be threatened because too many others would end up paying the costs of gregariousness. Group stability would quickly be threatened, leading to the rapid collapse of these social contracts (Nonacs, 2001). There are many evolutionary conditions that counteract these effects and produce cooperative behaviour (Hamilton, 1964; West et al., 2007).

The real issue seems to be the cognitive demands of maintaining the stability of social relationships through time. This process of negotiation seems to be very complex. It requires coordination and compromise, and often adjustments to ensure that group members do not drift apart during foraging. It also requires the ability to manage conflicts because they cause groups to dissipate, and to cope effectively with the ever-present threat generated by rivals. Perhaps it requires individuals to be able to understand another's perspective well enough to appreciate what kind of adjustments are necessary to create the levels of "bondedness" required to keep a group together. One element of that is knowing when to trust another individual. Therefore what is called the "top-down" approach starts with the question of what cognitive abilities are needed to create "bonds" between individuals as a basic requirement for the social contract. The top-down approach tries to explain the evolution of social structures by the evolution of the cognitive abilities of the individuals these social structures are composed of.

The main problem of this approach is, that the process is explained by its result, not by its causes. The cognitive abilities could be a result of the evolution of social structures. It might be necessary to view the evolution of social structures as co-evolution of social cognition and socialisation.

Instead of the top-down approach of analysing the cognitive abilities assumed to be necessary as precondition for social structures, there is also the possibility of a bottom-up approach. The central question of a bottom-up approach would be: "What facilitated the evolution of gregariousness and dominance in the first place?" In order to answer this question it is necessary to explore the effects environmental constraint like predation and food availability have on group formation. If these factors lead to the evolution of gregariousness, as discussed in section 2.2, it is possible that the evolution of cognitive abilities, which enable social coherence or "bonding" between individuals is a result of this selective process. The main goal of a bottom-up approach is therefore to explore what environmental conditions favoured a selection towards group living and social dominance. This

thesis and the models presented in it follow the bottom-up approach.

## 2.9 Summary

Dominance hierarchies can be viewed as one way of limiting aggression within social groups. Both dominant and subordinate animals would benefit from such hierarchies by reducing the costs associated with aggressive behaviour (Tinbergen, 1951). Alternatively being dominant or being subordinate could be separate strategies adopted on an individual level and could therefore be viewed as an adaptive solution for solving a conflict via a mixed evolutionarily stable strategy (Maynard-Smith, 1982).

These two perspectives are the starting point for a couple of questions concerning the origin and evolution of dominance behaviour, its role in group-level processes and the role of individual recognition and memory during agonistic interactions. This is where the problem of understanding social evolution starts to show its complexity.

This chapter presented different background theories explaining the reasons for the existence of social groups. It started by examining the reasons for group living following Hamilton's theory (Hamilton, 1971). According to him predation played the initial role for the process of group formation, but other factors like food and its distribution and offspring protection seem to be also important for the evolution of gregariousness.

The role of vigilance is explained as well as the possible function of social dominance. At the end of the chapter the two different approaches to social evolution are briefly discussed. This was necessary because the rest of this work will deal with the bottom-up approach by analysing different environmental constraints and their possible effects on the evolution of gregariousness and social dominance.

In the next chapter different theories concerning the reasons for the existence of different social structures observed in different primate species will be discussed in more detail using genus *macaca* as example. The socio-ecological theory and

the phylogenetic inertia theory will be examined, because the socio-ecological theory was the starting point for the model discussed in chapter 7.

# Chapter 3

## Social organisation in primates

### 3.1 Introduction

In this chapter two of the main theories explaining the existence of different social structures observed in different species of primates, particularly in macaques, are discussed. They both deal with egalitarian and despotic social structures but explain their existence differently. The similarities and differences between the two theories will be explained. One of the two theories, the socio-ecological theory was the starting point of the model discussed in chapter 7. Also in this chapter a first overview of the one already existing ABM environment called *DomWorld* will be given and the theory and assumptions of this modelling environment will be introduced. This theory and the modelling environment are the base of the first model presented in this thesis in chapter 5. This model represents an replication of *DomWorld*.

One of the problems of behavioural observational research is the reliable description of behavioural patterns observed and the definition of comparable categories for each of these behavioural patterns. Tinbergen (1963) proposed four factors by which observed behaviour should be described: immediate factors, ontogenetic development, adaptive functions and evolutionary history. These four factors should enable researchers to give a thorough description of the behavioural phenomenon in question. Tinbergen's categories are usually described in terms of proximate and ultimate causes (Mayr, 1961). Additionally in biology proximate



causes are looked at as emerging and facilitating ultimate causes.

Ultimate causes of behaviour are all the processes which are determined by the genetic structure of the organism. These causes are for example certain hormonal levels which trigger different responses to certain environmental cues. Proximate causes of behaviour are everything that shapes the interaction patterns and personal traits of an individual during its life time. These are for example learning or cultural transmission.

Even though on first sight Tinbergen's four factors and the differentiation of proximate and ultimate causes seems to be a good system for sufficiently describing the observable behavioural continuum, it has its limits (Dewsbury, 1992; Thierry, 2005). The biggest problem is determining exactly what are causes and what are consequences of a behaviour. Like in any other complex problem the multitude of possible explanations caused by numerous feedback loops challenges the human ability to fully understand the causal relationships between the different phenomena inherent in the problem. Nevertheless, since Tinbergen first came forward with his four questions a wide variety of different approaches to understanding especially primate behaviour have been established.

## 3.2 Macaques as a model species

As mentioned in the beginning of this chapter the goal one of the models presented in this work is the comparison of socio-ecological theory and the phylogenetic inertia theory. This model, which is called the **Macaque Social Interaction** model and will be discussed in chapter 7, is based on research results from genus *macaca* (Thierry et al., 2004). The genus *macaca* was chosen for this task for a variety of reasons:

1. Genus *macaca* contains of 22 different species living under very diverse environmental conditions and having very different social organisations ranging from egalitarian to despotic (Thierry et al., 2004).
2. The different species of the genus *macaca* have been the subject of extensive comparative behavioural research over the last thirty years and as a result

we have a good understanding of the differences in social structure between different species.

3. This data is sufficient to test the two theories I wanted to examine with the **Macaque Social Interaction** model.

For a long time behavioural research on macaques focused on the general description of the different species and on observations with the focus of conservation. With the accumulation of knowledge about their social interaction patterns scientist started to realise that they had different behavioural repertoires. Until that point it was thought, that their behaviour repertoire had to be similar, because their cognitive abilities are largely the same.

This changed during early 1980's when the ecological theory of social interaction was postulated (Wrangham, 1980; van Schaik, 1983, 1989) inspired by the work of Hamilton (1971). In this theory it was proposed, that the social style in which individuals of a species interact with each other is flexible and that it depends on the environmental conditions a species lives in.

To find evidence for this theory in nature the genus *macaca* with its species distributed in different types of habitats around the old world became the perfect subject. Following this line of thought the behavioural research on different species of macaques became increasingly comparative taking the differences in the habitats the animals lived in into consideration (Thierry, 1985; de Waal, 1989; de Waal and Johanowicz, 1993). Dunbar (1991) and Chapais (2001) examined the functions of certain behaviours like grooming or nepotism in the social context. They could show that different species use different social techniques in certain contexts to solve tensions between group members. With the advance in this research a detailed understanding of the role of social dominance became more and more important. This will be discussed in detail later in this chapter.

Thierry started to work on within group interactions between males and females in rhesus (*macaca mulatta*) and tonkean macaques (*macaca tonkeana*) in the middle of the 1980's (Thierry, 1985, 1986b,a). He postulated that different macaque species have different social styles based on their inter-individual tolerance levels and classified these social styles according to different behavioural characters into four grades (see table 3.1) ranging from despotic (Grade 1) to egalitarian (Grade 4).

Grade 1	Grade 2	Grade 3	Grade 4
Macaca mulatta	Macaca fascicularis	Macaca sylvanus	Macaca tonkeana
Macaca fuscata	Macaca nemestrina	Macaca silenus	Macaca maurus
Macaca cyclopsis		Macaca arctoides	Macaca nigra
		Macaca radiata	Macaca nigrescens
		Macaca assamensis	Macaca hecki
		Macaca thibetana	Macaca ochreata
		Macaca sinica	Macaca brunnescens

Table 3.1: Classification of Macaque species based on their social styles. Interindividual tolerance increases from Grade 1 to Grade 4. The most despotic behaviour is therefore shown by the species of Grade 1 (Thierry et al., 2004, p.274).

Other researchers examined the influence of different hormone levels on the intensity and type of social behaviours displayed by a variety of different primate species in certain situation (Aujard et al., 1998; Michael and Zumpe, 1993). At the beginning of the 1990s the scientific community had a very good understanding of the social ecological situation and sufficient data to start to analyse the reasons for the differences in the observed social behaviour patterns. Two theories about the reasons responsible for the existence of different social styles are the *Phylogenetic Inertia Theory* (hereafter PIT) by Thierry (Thierry et al., 2004), saying that the differences are mainly based on random variation and that environmental changes only play a secondary if any role, and the *Socio-ecological Theory* (hereafter SET) by van Schaik (van Schaik, 1996) saying that primarily environmental pressures are responsible for shaping the evolution of these different social styles. These two theories will be analysed and tested for coherence with the model presented in chapter 7.

Another theory by Hemelrijk (1999b, 2002a) deals with the underlying mechanisms of a possible transition from a more egalitarian towards a more despotic social structure. In order to test her assumptions she has created a modelling

environment called *DomWorld* and ran a number of agent based models inside this environment. Hemelrijk assumes, like the PIT, that the phylogentic heritage of a species is the primary reason for the social structure exhibited by this species. She also assumes, based on the evidence brought forward by the PIT, that despotic social structure derived from egalitarian social structure and that therefore the latter is the original form.

In this chapter these theories will be discussed in detail, because they represent the empirical background for my models. I will start by defining what is meant by social style in genus *macaca*.

### 3.2.1 Different social styles in the *Genus Macaca*

In order to approach the problem of how different social styles evolved it is necessary to define what is meant by “social style”. Social style is defined as the variety of behaviours an individual exhibits while interacting with other members of its own species. In other words how many distinguishable different action patterns an individual uses in a social context. This includes, besides how frequently and intensely a behaviour is executed, also how large the behavioural repertoire of an individual is.

A distinction between egalitarian and despotic social style was first drawn for different bird species (Vehrencamp, 1983). The definition of the difference in social structure was in this case based on the reproductive success of these birds. More egalitarian species were defined as species in which all individuals are equally successful in raising offspring, more despotic species as being characterised by a big variance between the individuals in their reproductive success.

In primates the distinction between different social styles is based on the dominance style of the different primate species (Hand, 1986). The dominance style is defined as the gradient of hierarchy (van Schaik, 1989). The steeper the group hierarchy of a species is, the more despotic the species. The steepness of the group hierarchy is operationalised as the way interactions between individuals in a group are carried out. The less tolerant the individuals are to each other proximity, the steeper is the hierarchy. A thorough examination and analysis of these different dominance styles for the different species of the genus *macaca* was

done by Thierry (e.g. Thierry, 2004).

Individuals of gregarious animal species influence each other with their behaviour and with the way they engage in social interactions. They inhibit or reinforce the execution of certain actions by performing facial cues or body movements. Even tactical considerations can be observed, at least in chimpanzees (de Waal, 2000). Individuals can be excluded from grooming or even collectively attacked, depending on their social status or alliances (Parker, 1974; Enquist and Leimar, 1983).

The simplest form of an aggressive interaction between two individuals is usually composed of a single threats or a sequence of threats followed by either an aggressive or submissive response from the addressed individual. These threats can be more or less pronounced and physical. The submissive behaviour contains in general reconciliatory reactions. For both, the aggressive and the submissive behaviour each species has a repertoire of possible actions. These actions usually express the seriousness of the executer in its intentions. The reaction to an aggression depends for example on the risk of getting injured in the possibly following fight. For a subdominant individual it is therefore better in a high-risk situation to submit than to counter attack.

The dominance gradient is a measure for the distance between individuals in the group hierarchy. The easier it is for subdominant individuals to retaliate, given the action repertoire of the species, the less steep the dominance gradient in this species (Preuschoft and van Schaik, 2000).

In other words in groups in which it is hard for individuals to retaliate highly intensive aggressive social interactions should be sparse, since they would lead to severe injuries and would therefore be a poor strategy. Mothers in such societies should severely restrict their offspring in order to limit their interactions with other individuals and prevent them from harm (Kenna, 1979; Thierry, 2000). These groups are defined as being despotic.

A variety of conciliatory actions enables the individuals to show submissive behaviour as response to a threat or aggression. These behaviours are not only shaped by environmental factors (section 3.4) but also by social processes. Such processes are for example social learning (Tomasello, 2000) or other forms of

inter-generational transmission. In such transmission for example the dominance status and the social network of the mother are passed to her daughters (Berman, 1982, 1990; de Waal, 1996).

An interesting finding concerning the plasticity of social behaviour comes from an experiment with juvenile rhesus and stumptail macaques. Both species have different social styles. In Thierry's categories rhesus monkeys are considered to be very despotic (Grade 1) and stumptail macaques are considered to be moderately egalitarian (Grade 3) (Thierry, 2004, 2007). Two groups of 4 juvenile rhesus macaque were housed together with in each case 3 older stumptail macaques. Very quickly the conciliatory tendencies of the young rhesus macaques increased to a level comparable with the older stumptail macaques (de Waal and Johanowicz, 1993), but they never completely adapted the entire egalitarian social behaviour repertoire. In particular, new reconciliation behaviours were not learned, but normal rhesus reconciliation behaviour was used at a greatly increased frequency. This change persisted after the rhesus juveniles were reintroduced to their original colony.

Due to the small number of individuals observed during the experiment and that there have been no comparable experiments the external validity of the experiment is rather small. But the lack of adaptability of the juvenile rhesus macaque to certain egalitarian social behaviours can be explained in two ways. Firstly genetic heritage has an influence on the behavioural repertoire of a species which determines its social structure. The genetic heritage influences the individual behaviour directly through different hormone levels and body size and also indirectly, because the behaviour of the individual shapes the behaviour of its conspecifics (Altmann and Altmann, 1979; Wolf et al., 1998). Secondly and probably more importantly the juvenile rhesus macaques were at the time of the start of the experiment already six months old. It might have already socially acquired the behaviours it could not change during a critical learning period. But the result suggests also that there is at least in young age a window of plasticity which enables the individual to adapt its behaviour to the social environmental conditions surrounding it.

### 3.3 The Phylogenetic Inertia Theory

As mentioned above Thierry (2000) defined a four-grade scale for the categorisation of macaque social structure. His grades are mainly based on patterns of aggression and reconciliation. The macaque species on grade 1 and 2 are considered to be more despotic, the macaque species on grade 3 and 4 to be more egalitarian.

Thierry defines a despotic species by high levels of aggression, low frequency of aggressive interactions and a less cohesive grouping due to strong differences in rank. The aggressive interactions in these groups are unidirectional and social behaviour is more correlated to social dominance than in egalitarian groups (de Waal and Luttrell, 1989; de Waal and Johanowicz, 1993; Thierry, 1985, 1990). Egalitarian species on the other hand are defined, according to him, by small rank differences, low levels of aggression, high frequency of both agonistic and reconciliation behaviour and many affiliative interactions (Thierry, 1984, 1986b, 1990).

Rhesus (*macaca mulatta*) and Japanese macaques (*macaca fuscata*) have been observed to be organised in groups where high-intensity aggression is common, reconciliation behaviour is infrequent and aggressions are mainly unidirectional (Thierry, 1985; de Waal and Luttrell, 1989; Aureli et al., 1993) and are therefore categorised as being despotic. Crested (*macaca nigra*), moor (*macaca maurus*) and tonkean macaques (*macaca tonkeana*) are organised in groups in which aggression is in general of low intensity, reconciliation is frequent and most of the conflicts are bidirectional even between individuals of very different ranks (Bernstein et al., 1983; Thierry, 1985; Petit and Thierry, 1994; Matsumura, 1996). They are categorised as being egalitarian.

The two social styles, despotic and egalitarian represent the two extremes of a continuum in Thierry's theory. Macaque species located on grade 2 and 3 still exert either despotic or egalitarian behaviours but are less pronounced in doing so. Longtailed (*macaca fascicularis*) and pigtailed macaques (*macaca nemestrina*) tend to be moderately despotic (Judge, 1991; Thierry, 2000) stumptailed (*macaca arctoides*) and liontailed macaques (*macaca silenus*) moderately egalitarian (de Waal and Luttrell, 1989; Aureli and Veeneman, 1997).

The question is why and how did this complex system of differentiated social

behaviours evolve. Different reasons have been proposed such as environmental changes in the habitats which led to isolation of certain groups and changes in food availability and predation pressure. Besides environmental factors selecting on the individual level, individual differences in character based on genetic random variation are thought to also have an influence on *how flexible different social behaviours can be used in different situations*. There is still a lot of argument about which is the more important factor influencing the behavioural repertoire of a species, environment or genetic heritage. The PIT sees the majority of the arguments pointing at the genetic heritage. The main argument for this assumption is the dispersal pattern of the genus.

### 3.3.1 Dispersal pattern of the genus *macaca*

The genus *macaca* represents a monophyletic group of the cercopithecine subfamily. Fossil record indicates that it originated in the Near East and colonised Eurasia around 5 to 6 million years ago (Thierry, 2007). It then branched into mainly three distinguishable phylogenetic lineages, which have been identified from the morphological and molecular data available (Fooden, 1982; Hoelzer and Melnik, 1996; Ziegler et al., 2007).

The three lineages are the *silenus*, the *sinica* and the *fascicularis* lineage. The *silenus* lineage can be found in the evergreen forests of southern India (liontailed macaque), on the Mentawai islands (e.g. pagai macaque) and on the Sulawesi islands (e.g. crested macaque). Due to the disjunct geographical distribution it is assumed that this lineage represents the successors of the first dispersal wave into Eurasia. The members of the species of the *sinica* lineage are thought to be the descendants of the second dispersal waves due to their moderately fragmented distribution in southern Asia. The species of this lineage are mainly found in the tropical and subtropical continental areas of south-east Asia. The species of the *fascularis* lineage have the most broad and continues distribution of the three lineages. They range from equatorial, tropical regions (longtailed macaque) to the mountainous, temperate regions (Japanese macaque) of Asia. The Barbary macaque living in the mountainous forest areas of north Africa with its habitat separated from all other species of the genus is thought to be the most ancient taxon (Delson, 1980; Fooden, 1976; Thierry, 2004, 2007).



Analysing the phylogenetic tree for the characteristics of the different social styles it is according to Thierry (2004) possible to reconstruct the typical ancestral social organisation. This ancestral social style should be closest to grade 3 of Thierry's scale. Following this conclusion it is very likely that the original social style in the genus was egalitarian. Barbary macaques as the most ancient taxon followed by Liontailed macaques which descended from the first dispersal wave. Both these species are on grade 3 of Thierry's scale. This is one of the premises of the assumption that egalitarian social structure has been the ancestral form social structure in genus macaca (Thierry et al., 2000). Since according to this assumption the original social structure was grade 3 on Thierry's scale, the development from it to today's social structures found in macaques went in both directions, to a more despotic and also to a more egalitarian social structure.

In summary the PIT assumes that the reasons for the differences found in the social structure of the different macaque species are mainly based on individual character differences which in turn are based on the genetic heritage of the species and that the effect environmental pressures have are a strictly limited by the preexisting genetic structure (Thierry, 2007). It also assumes that the plasticity of these social structures is rather small and that therefore changes in the social structure of a species can happen only slowly and are traceable throughout its genetic history.

The SET on the other hand emphasises the influence of environmental pressures on social structure. It postulates that the environmental conditions surrounding a species shape the way the individuals in this species interact with each other.

### **3.4 The Socio-Ecological Theory**

Wrangham (1979) suggests that ecological factors have a more direct influence on social relations among females than on social relations among males or between males and females. He suggested that male spatial distribution depends on the distribution of the females mainly for reasons of mating competition and mate choice. He categorised multi-female groups of primates into female-bonded and nonfemale-bonded (Wrangham, 1980). According to his theory female-bonded groups evolved as a result of food competition for high quality food patches in

an environment with a limited number of feeding sites. Under such conditions females needed to form and stay in groups with their kin as reliable coalition partners to defend their food cooperatively against other groups. They are therefore surrounded by genetic relatives and maintain strong grooming bonds. According to this theory female-bonded groups should mainly be frugivorous and non-female-bonded groups would be folivorous, since seasonal fruits which grow on a limited number of trees are easier to defend cooperatively than leaves that grow on every tree all year around. After a couple years of research it turned out that Wrangham's theory was not entirely right and was not supported by many empirical results (van Schaik, 1983; Dunbar, 1988).

### **3.4.1 Food-type, food-availability and food distribution**

Carel van Schaik (1983, 1989) extended Wrangham's theory, mainly in two ways. He classified within-group competition for food in more detail by dividing it into within-group-scramble and within-group-contest and he also took predation risk into account. According to Nicholson (1967) there are two possible forms of competition for food among animals: scramble and contest. Scramble occurs when all animals share the same food supply in such a way that any particular individual is unable to prevent other individuals from getting the same amount of food as itself does; this depends highly on the spatial distribution of the food sources. On the other hand whenever it is possible to monopolise food, competition will be by contest. This will turn some individuals into winners which will make them resource owners and help them to obtain a greater share of the food than the losers. In most environmental conditions animals will experience a combination of both forms of competition (van Schaik, 1989). Predation pressure is thought to be the initial reason for the evolution of gregarious life style (Hamilton, 1971). In the SET it is besides food availability the other major environmental pressure forcing females in non-human primates to live in groups.

The two forms of food competition can be combined with the within and between group conditions resulting in four different types of competition in non-human primates (Janson and van Schaik, 1988):

1. Within-group scramble (*WGS*):

Occurs if individuals live in an environment with either very small food items (e.g. insects) or very large (relative to the group size) food patches.

2. Within-group contest (*WGC*):

Occurs if the food in the environment is distributed in well-defined patches and enables some of the group members to monopolise it. This form of competition should be found in frugivorous animals.

3. Between-group scramble (*BGS*):

If two groups of the same species share the same area extensively and suffer equally from each others' removal of the food this form of competition should be found.

4. Between-group contest (*BGC*):

This should occur if the members of the more dominant group replace members of the other group and the subdominant group starts to avoid encounters with the dominant group. This then results in one group obtaining more food than the other.

Because *BGS* occurs only if groups occupy more or less exclusive ranges, it has no influence on inter-individual behaviour. It represents the effect of population density on net food intake and would be overridden by the effects of *BGC* if they occurred together in an environment. It therefore has no effect on female social relationships (van Schaik, 1989).

This leaves three conditions which can either have a weak or strong effect on individual interaction patterns. All three conditions combined, as would be most likely in nature, and taking in consideration that they can have a strong or weak effect on the individuals, the result are eight possible combinations. The combination of strong or weak effects in all three conditions at the same time is highly unlikely in the natural environment as is the occurrence of *WGC* and *BGC* in combination with weak *WGS*. Since the effects of contest always override the effects of scramble, the combination of weak *WGS* and strong *WGC* and the combination of strong *WGS* and strong *WGC* can be viewed as the same. This leaves us with four possible combinations which can have an influence on the social interactions of non-human primates. In his theory van Schaik (1989) calls these combinations "Type A", "Type B", "Type C" and "Type D" (Tables 3.2 and 3.3).

Form of competition	Type A	Type B	Type C	Type D
within-group scramble	strong	weak	strong	weak
within-group contest	weak	strong	weak	weak
between-group contest	weak	weak	strong	strong

Table 3.2: Possible combinations of different forms of food competition following van Schaik (1989)

### Strong within-group scramble

**Type A** can be described as strong within-group scramble only and is found among primates living in environments with a high risk of predation and with a diet of leaves and/or insects. The food is dispersed over a large area or in clumps large enough for the entire group to feed together. This implies the population density may be lower than the carrying capacity of the environment, generally as a result of predation. The social organisation is egalitarian. In an environment like this, the only pressure that keeps the group together is the predation risk. Females don't have to build up close social networks with their genetic relatives since they suffer only little pressure from within the group. They could migrate in little groups more or less freely from one large group to the other. This means they can be resident and that new groups are founded by troops of migrating females which then allow young males to join them. Gorillas (*gorilla gorilla*) are an example of this social strategy (van Schaik, 1989). Macaque species have not been found to live under such environmental conditions.

### Strong within-group contest

**Type B** can be described as within-group-contest only. This occurs in conditions with high predation risk and in primates with a frugivorous or omnivorous diet. The animals feed on fruit or basically everything they can find that is edible and possible to hunt. The food in this condition occurs in small patches,

is monopolisable and the amount of food within the patches is smaller than the group would need. The population density on the other hand is smaller than the environmental capacity, but the animals are restricted by the high predation pressure from moving freely in the habitat. The resulting social structure is despotic and nepotistic. Females build strong bonds with genetic relatives in order to form coalitions and withstand the pressures from inside the group. Wherever possible strong individuals monopolise resources. Females need to be resident to form their bonds and new groups are formed by the process of group splitting, once the number reaches the point where a certain number of individuals would not be able to survive with the restrained resources. Examples for this strategy are rhesus macaques (*macaca mulatta*) and longtailed macaques (*macaca fascicularis*) (van Schaik, 1983, 1989), which are both classified as despotic species by Thierry (Table 3.1).

### **Strong within-group scramble and strong between-group contest**

In **Type C** strong within-group scramble and strong between-group contest are the predominant social pressures that shape the interaction patterns of the group. Under these conditions the predation risk ranges from intermediate to high and the animals are frugivorous or omnivorous. The food occurs dispersed or in clumps. The clumps in this conditions are just big enough to be monopolisable on the group level and the population density matches the environment capacity. This is the reason for the between-group contest. The social style is egalitarian, but due to the pressure from other groups the females stay resident. The formation of new groups is restricted also due to the saturation of the environmental capacity. Examples for this type are different subspecies of the *genus presbytis* (van Schaik, 1989). Macaque species have not been found to live under such environmental conditions.

### **Strong between-group contest**

**Type D** can be described as strong between-group contest only. In this environment the predation risk is low and the animals are frugivorous or omnivorous. The food occurs clumped and is monopolisable on the group level. The population density matches the environment capacity and the females are resident. This

leads to an egalitarian and nepotistic social structure. Nepotism in primates is defined as kin-directed beneficence (Moore, 1992). The cohesiveness of the group would be less than in type C due to the absence of predation. The formation of new groups is restricted due to the saturation of the environmental capacity. Examples for this environmental conditions are crested macaques (*macaca nigra*) and bonobos (*pan paniscus*) (van Schaik, 1989), which are classified as egalitarian species by Thierry (Table 3.1).

### 3.4.2 The influence of predation

Besides food availability and food distribution there are a variety of other factors thought to have a strong influence on the evolution of social behaviour. The effects of these factors have been discussed separately, but they are also discussed in the socio-ecological theory. One of these factors is predation.

As discussed in section 2.2 predation is thought to be the initial reason why animals live in groups (Hamilton, 1971; van Schaik, 1983). Animals group to increase their safety. The likelihood of falling victim to a predator decreases with the number of individuals in a group (Hamilton, 1971). This is true for most terrestrial animals.

Predators usually attack single individuals or individuals which are far away from other members of their group (Hamilton, 1971). The position of these animals in their groups is usually at the fringe, because this is where they are furthest away from everybody else. This makes spatial centrality an important factor for the selection of dominance. If a dominant individual in the centre of a group is surrounded by many peripheral subordinate individuals, its probability of getting eaten is smaller than the probability of the subordinate individuals. In savannah-living primates like the yellow baboon (*papio cynocephalus*) females tend to be surrounded by as many other group members as possible to increase their safety. High-ranking dominant females are observed to be most of the time in the centre of the group (Collins, 1984).

The main predator for terrestrial primates are leopards and lions. In field research the event of a primate killed by a predator is seldom observed, probably due to the presence of the observer distracting the stalking process of the predator

Type	Competition Regime	Population Density	Diet	Predation Rate	Food Distribution	Hierarchy	Social Organisation	Examples
A	within-group scramble	$PD^a < ECC^b$	folivorous insectivorous	high	dispersed or clumped	egalitarian	individualistic	Gorilla gorilla
B	within-group contest	$PD < ECC$	frugivorous omnivorous	high	clumped	despotic	nepotistic	Macaca mulatta
C	within-group scramble between-group scramble	$PD = ECC$	frugivorous omnivorous	intermediate	dispersed or clumped	egalitarian	individualistic	Genus presbytis
D	between-group competition	$PD = ECC$	frugivorous omnivorous	low	clumped (on group level)	egalitarian	nepotistic	Macaca nigra

Table 3.3: Summary of socio-ecological theory (van Schaik, 1989)

<sup>a</sup> $PD$  = Population Density  
<sup>b</sup> $ECC$  = Environmental Carrying Capacity

(Zuberbühler and Jenny, 2002). But decreasing numbers in groups exposed to environments with increased predation illustrate the effect predation has.

Hill and Dunbar (1998) suggest that: "... an understanding of the role of predation as a selective pressure on primates will only be achieved by attempts to study the factors that are important in determining a primate's perceived risk of predation". Predation also has an impact on primate behaviour if there are no predators immediately present. Primates perceive the potential predation risk in an environment and act accordingly. But the process by which this is achieved is not further discussed in the literature. Nevertheless the theory is interesting since it explains the maintenance of groups in the absence of predators.

In summary predation has according to Hamilton and most empirical research, two effects. It acts as cohesive force keeping groups together, and in doing so make the centre of the group the safest place.

### **3.4.3 Other factors influencing the development of social structures**

#### **Group size**

Sterck et al. (1997) added group size as another possible factor that influences social structure into Wrangham's and van Schaik's models. There is a dynamic relationship between the group size and the group's growth rate. The lowest number of individuals to form a group is the minimum viable group size (Sterck et al., 1997). This is the size in which individuals in the given environmental situation just manage to survive and to reproduce. If the number drops below that point, the group dissolves. At this point cooperation between the individuals will be vital for the survival of the group.

If the group is successful its members will start to reproduce until they reach the maximum group size. The maximum group size is the equilibrium between the number of individuals in a group and the carrying capacity of the environment. If the group size grows above it the group fissions, decomposing itself into smaller new groups.



The connection between group size and social structure is competition for limited resources, because competition increases with the increasing group size. This is due to decreasing food access in groups with an increasing number of members. Group size is an additional but dependent factor of food distribution and predation risk. The interaction between group size, predation pressure, food availability and food distribution is reflected by population density.

### **Infanticide risk reduction**

Another important external environmental factor which forces females to live in groups is infanticide risk. Observations show that infanticide by males can be a major source for infant mortality (Hrdy et al., 1995). Infanticide by males is thought to be an evolved reproductive strategy (Struhsaker and Leland, 1987; Newton, 1987; Bartlett et al., 1993; Sterck et al., 1997). It increases the reproductive success of the males because by killing the infant and disrupting the lactation period the female will be faster receptive again. Since the killing of the infants lowers the reproductive success of the females, they had to evolve strategies to defend their infants from becoming the target of male aggression. Some form female coalitions to protect each other (Hrdy, 1979; van Schaik, 1996), but the best way is to associate with males permanently (van Schaik and Kappler, 1993), who in turn then can be the fathers of the infants. It is possible that one factor for the explanation of female dispersal patterns is the reduction of infanticide risk (Sterck et al., 1997; van Schaik, 1996). Females in multi-male multi-female groups share male anti-infanticidal services (Sterck et al., 1997). Together with the predation risk this could explain the composition of male-female association in gregarious primates.

## **3.5 Differences between PIT and SET**

The main difference between PIT and SET is the explanation of the reasons for the evolution of different social structures in primates species. As mentioned above Thierry proposes that the phylogenetic history of a species is more important than environmental pressures and that it defines the way the individuals of a species interact with each other. According to the PIT the behavioural differences

between different species are largely based on random genetic variation (Thierry, 2004). The SET on the other hand claims that the primary reason for the differences in social structure are environmental pressures. It examines the effect of a variety of these environmental factors and their interaction effects, but mentions like Hamilton (1971) before food and predation to be the most important ones.

Another difference between these two approaches is the way despotic social structure and egalitarian social structure is characterised. From these characteristics the description of the spatial distribution of more egalitarian and more despotic species shows the biggest difference. Thierry describes the individuals in despotic species as being further apart from each other, because the subordinates avoid confrontations with the dominant individuals (Thierry, 1986b, 1990). He also describes individuals in egalitarian social groups as being in close proximity to each other, because of their high frequency in affiliative interactions (Thierry, 1985, 1990). Van Schaik reports that groups with despotic social structure are more likely to be found in environments with high predation pressure, because the predation forces the individuals to stay closer together and due to the limitation of space, they start to become more aggressive (van Schaik, 1989). Following the SET more egalitarian primate species should be found in environments with low predation pressure (Table 3.3), which in turn should allow them to have a wider spatial structure.

A decrease of the inter-individual distances between the individuals of a group caused by an increase in predation pressure is also one of the predictions of Hamilton's theory (Hamilton, 1971). It is very likely that a decrease in inter-individual distance leads to more aggression, especially because of the *centripetal instinct*. Predators kill individuals on the fringe of the group, therefore the safest place is the centre of the group. If all individuals try to gain a central position, because it is a valuable resource, it is possible that this will result in higher levels of aggression. I will explore the difference between the SET and the PIT in chapter 9.

### 3.6 Hemelrijk's DomWorld

Hemelrijk (1999b, 2000, 2002a) constructed a model called *DomWorld* in order

to test a variety of factors which could have an influence on the transition from one social structure to another. In doing so she uses different assumptions from the PIT and the SET. The most important assumption is that egalitarian and despotic social structures do exist in different primate species. This seems trivial, but it has been subject to discussion for a long time and at least the characteristics of these groups are controversial (van Schaik, 1989; Thierry, 1990, 2004).

Hemelrijk also assumes that egalitarian social structure preceded the despotic structure based on e.g. Matsumura (1999) and Thierry et al. (2000). Although her theory includes statements of the PIT, she also uses the conclusions from the SET about the influence of environmental factors on social behaviour as starting point for her hypotheses about the reasons for the evolution of social structure. One of her hypotheses about the reason for the shift from egalitarian to despotic social structure is that if food is scarce, a group of despotic agents has a better chance to survive, because the most dominant individuals will obtain enough food to reproduce whereas in groups with a weaker hierarchy most agents will get an equal share, which means none of them will obtain enough food to reproduce (Hemelrijk, 2002b). The shift from egalitarian to despotic social structure therefore happens (assuming egalitarian social structure is phylogenetically older) if an egalitarian group moves from an environment with a lot of food to an environment with limited food resources. In such a case individuals with more aggressive tendencies would start to be selected for and as a result the group would change successively into being more despotic (Rypstra, 1993).

An additional factor probably accelerating this process is food distribution, as already hypothesised by van Schaik. If the food is clumped, dominant individuals profit because they can monopolise it. If the food is scattered, everyone can get its share and the social structure stays egalitarian (Nicholson, 1967; Hemelrijk, 2002b).

Another reappearing topic in her work is female dominance. Her main interest concerning this question is to answer how females can manage to become dominant over males in their groups, despite the bigger size and higher aggression levels of the males. In various studies (e.g. Hemelrijk, 1999a; Hemelrijk et al., 2008) she shows that female dominance could occur as a side effect of sexual attractiveness due to higher interaction frequencies in combination with the so called winner-loser effect. This will be discussed in detail in chapter 5.

In summary it can be said that Hemelrijk proposes that complex social structures can emerge due to self-organisation based on a complex feedback process between the different individual characteristics of the agents (Hemelrijk, 2003). These social structures do not necessarily need to be based on higher cognitive function or genetic heritage (Hogeweg, 1988), but are a possible emergent phenomenon of a complex system. The replication of one of her models (Hemelrijk, 2002a) will be discussed in detail in chapter 5.



# Chapter 4

## Agent-Based Modelling

This chapter gives an overview of agent based modelling, its scientific background and compares it to the more classical approach of equation-based modelling. Furthermore the problems of integrating ABM into social sciences is explained from the perspective of developing and controlling complex agents. The problems encountered in the process of implementing the models in this thesis are discussed as well as the ways they were solved.

Assuming complex social interaction patterns are the result of individual decision making, there is the problem of how an individual decides what to do next. Part of this problem, called action selection, is the question of how can action selection plans be flexible enough to enable agents to finish an action or switch behaviour during current actions. At the end of this chapter an example of an agent architecture will be discussed, including a mechanism for reacting quickly to changes in the environment while pursuing a goal. This discussion will build a link to the application of ABM in primatology.

### 4.1 What is Agent-Based Modelling

ABM is a computer simulation method for testing the collective effects of individual action selection. More generally, ABM allows the examination of macro-level effects from micro-level behaviour (Bryson et al., 2007). With ABM it is

possible to build agents with individual characteristics and then monitor the effect individual behaviour has on a group level.

ABM is in some ways the opposite of statistical population modelling. In population models all agents are exactly the same. Such models enable researchers to understand the dynamics of groups on a macro level. Population models are usually used to model ecosystems in order to answer questions on a global scale.

But often in science researchers want to understand how the observed characteristic of a system can be accounted for by its components. In ABM the building of models of both the components and the environment they exist in is possible in order to see whether the over-all system-level behaviour of the model matches that of the target (or *subject*) system. Agent based models enable us for example not only to look at what impact an ant population has in a certain environmental setting, but also what is going on inside the anthill. In this dissertation ABM is used to model the interactions of the individual monkeys inside their group, by giving each monkey different states, and resulting from this different possible actions to select, in order to solve the problem at hand.

ABM is a sufficiently new technique that there is still some controversy about its use, and still some unevenness in its application and description in scientific papers. Most critically, there is not enough methodological practice established in incorporating modelling results into the scientific discourse. It is therefore important to develop a procedural plan for the usage of agent based models and the techniques for their analysis.

#### **4.1.1 Historical background of ABM**

The history of ABM starts with the urge to better understand human economic behaviour. Axelrod and Hamilton (1981) first started to use ABM for their evolutionary simulations of cooperative behaviour (Axelrod, 1984). Axelrod still is considered one of the area's main advocates as well as practitioners. Around the same time a first attempt to model animal behaviour was made with what was called an individual oriented model. Hogeweg and Hesper (1983) modelled the behaviour of bumble bees using what they called the *MIRROR modelling strategy*. The architecture of this approach dates back to their earlier work on simulation

structures (Hogeweg and Hesper, 1979). The model of Hemelrijk replicated in this thesis, DomWorld (Hemelrijk, 1999b) is based in this work.

In the appendix of a recent text on the use of agent based models in social science Axelrod and Tesfatsion (2005) describe four research goals for the field:

- *empirical:*

“Why have large-scale regularities evolved and persisted, even when there is little top-down control?”

- *normative understanding:*

“How can agent-based models be used as laboratories for the discovery of good designs?”

- *heuristic:*

“How can greater insight be attained about the fundamental causal mechanisms in social systems?”

- *methodological advancement:*

“How can we provide ABM-researchers with the methods and tools they need to undertake the rigorous study of social systems. . . and to examine the compatibility of experimentally-generated theories with real-world data?”

These questions illustrate that the main field of application for ABM is social science and that ABM can help to understand the evolution and maintenance of social systems based on inter-individual behaviour. The biggest methodological issue is how to properly compare empirical findings with the results from the simulations. This question is not only confined to agent based models, but to all kinds of models and has also strong philosophical implications which are discussed in detail in section 10.

## 4.2 When and why use ABM

ABM provides a possibility of finding answers to complex questions like how do environmental pressures influence the evolution social structures in groups,



because it is a bottom up simulation technique. The difference between bottom-up and top-down approaches in behavioural research are discussed in section 2.8. Due to this possibility of modelling agents with individual characteristics interacting with each other in the same environment, ABM has been used in the past mainly in economics and sociology. All the applications in these fields deal with current states of social interactions under changing conditions. The focus of the work presented in this dissertation is the evolution of social behaviour. The question to answer is not “how do individuals interact with each other”, but “why do they interact in the way they do”. As mentioned before, the goal of this work is to broaden and advance the usage of ABM into biology and anthropology and make it easier for researchers to apply it to their research questions.

The opposite of individual or agent based models are population or equations based models. These models focus on the analysis of the dynamics between large groups of entities and for example the environment. Their advantage is the restriction to a defined set of variables describing everything in the model which makes them useful for examining for example population ecology. The biggest disadvantage of population models in sociology is that they do not take individual variability into account (Grimm, 1999; Axtell, 2000).

In summary it can be said, ABM is useful in scientific fields in which it is important to understand a process itself and not only its result. This is due to the fact that agent based models work on a different level (with a different focus) than population models and because in order to understand inter-individual processes it is necessary to ask entirely different questions compared to the questions we need to ask in order to understand the processes underlying population dynamics.

#### **4.2.1 ABM in the scientific process**

In order for a methodology to be useful to science, it must provide two things: first a means of explanation, and second, a mechanism for improving that explanation (Bryson et al., 2007). The answer it gives to a question must be falsifiable and its explanatory value must be as high as possible. Like any other theory it needs to be open to public discussion (in the case of a computer based model the code must be publicly available) in order to be verifiable.

While introducing a new methodology its utility has always to be considered. How costly is it to implement the methodology and how much better or how much more does it explain a given question. The utility of simulations for example in biology or evolutionary anthropology is very high. Compared to the cost of conducting experiments with real animals or humans, the use of simulations is rather cheap. The main costs lie in the development of the model and in the comparison of its results with empirical findings. Once the simulation runs it can be modified and several different questions related to the problem in question can be examined with it. Another big advantage of such simulations is that they enable the researcher to relatively quickly test given hypotheses and maybe adjust their presumptions before these hypotheses are tested in natural settings. This spares a lot of time and money compared to an adjustment of false theories after their empirical testing.

The explanatory value of agent based models is in the extent to which an observed meta-level phenomenon can be accounted for by the behaviour of its micro-level actors. Agent based models are tested by sampling the behaviour of individualised agents both over time and over a number of repetitive runs. Also in different experimental runs either the same parameters may be used, in order to discover the range of possible results due only to the effects of random variation; or the parameters may be varied systematically, to test the significance of each parameter or *condition*.

The last and very important step is the comparison of the behaviour of the modelled system with the behaviour of the target system. In order to be able to meaningfully interpret the results of the simulation a thorough analysis of the empirical problem is essential. Both for the development and for the analysis and interpretation of the model a close connection between field research and theoretical work is necessary. Of course this will not completely prevent the occurrence of misinterpretation and incomplete theories, but it will make them at least less probable. This and the more frequent use of ABM in the social sciences and particularly in business and public policy are the reason for a increasing emphasis on developing methods of their verification and validation (Balci, 1998).

*Verification* is the process of making certain a model runs as designed. It is equivalent to ensuring that good experimental practice has been followed in empirical research. In the case of modelling this includes the debugging process of

the model and the systematic testing of all the interactions between the different variables in the simulation. In other words it is the answer to the question “Does the model what it is supposed to do?” Being systematic during the implementation and cautious while integrating new variables is the key to a manageable verification process. In order to make it possible for other scientists to comprehend how ideas and theories are integrated in the model a full documentation of the implementation process is very important. Even if some ideas seem to be straight forward and obvious to the programmer, this does not mean they are to everybody else in the scientific community. If a broader use of simulations in the scientific process is a desirable goal, it will be necessary to be very specific about these problems. Computer scientists and empirical researcher usually have very different perspectives on the same problem, and without proper communication misunderstandings will occur even in this first phase of making sure the model produces meaningful results.

After having verified the model the next step is its *validation*. *Validation* is the process of making certain the model actually models the target system. When ABM is used in biology, validation is equivalent to hypothesis testing. The common perception is that agent based models are so complex (in the sense of their number of parameters) that they can be made to easily match any data or predict any outcome and the model has no capacity for generalisation and therefore no predictive power. In practice, however, building and debugging agent based models is a difficult skill, as is matching data sets (Bryson et al., 2007).

If a model is built to a set of justified assumptions, and *subsequently* matches a data set with minimal adjustment, then it is generally considered to be at least partially validated. Of course, the more data sets it matches, the better the general validity of the model. But validation is not simply a state that either holds or does not for a model. Like any scientific hypothesis a model becomes more *likely* the more it is validated, but it never becomes perfectly certain (Box, 1979). The only exception is if a model becomes understood to such an extent that it can be *proven* correct in a logical or formal analytic sense.

Many people see formal analytic models as preferable to agent based models for this reason, but there are several reasons to use ABM. First of all, even formally correct models can be wrong if their premises or assumptions are incorrect (Bundy et al., 2005). Agent based models with their more experimental approach

can actually help to *verify* a *valid* model. Secondly, agent based models are very often more accessible or intuitive. Such models can consequently play an important role in scientific understanding, including *developing* a formal analytic understanding of a system by helping to explore the space of possible solutions (Axtell, 2000). And finally, there are large classes of dynamic systems which are not amenable to closed analytic solutions (Axelrod, 1997; Axtell, 2000). Particularly interesting to biologists are those involving the open-ended co-evolution of multiple interdependent species.

Returning to the matter of *verification*, this issue is most problematic in purely formal systems, where validation is not grounded in empirical data. Formal systems are used in mathematics and similar disciplines as a mechanism for knowledge discovery, and therefore verification is both more critical and more difficult. When validation is performed via hypothesis testing against empirical data, validation itself serves as a form of verification. Part of this process can be simplifying or generalising the model, or better determining the biological correlates of its components. This is true not only of ABM, but of all sorts of formal modelling in biology.

#### **4.2.2 Comparing ABM with equation based modelling**

ABM is characterised by a high degree of localisation and by discrete decisions. Equation based models are mostly applied to systems that can be modelled centrally. Agent based models include explicit case comparisons, while the dynamics in equation based models are dominated by physical laws rather than information processing.

The best modelling approach depends on the given problem. Both approaches simulate theoretical assumptions by constructing a model and executing it on a computer. The difference is how the model is executed. An agent based model consists of a set of agents that encapsulate the behaviours of the various individuals that make up the system. The execution of an agent based model consists of the emulation of individual behaviours. In equation based modelling, the model is a set of equations. In this case simulation means evaluating the state space of the set of equations. The validation of both types of models is done by comparing the output of the model with the system behaviour in reality. Additionally

to this agent based models can also be validated on the individual level. The behaviours encoded for each agent can be compared with local observations on the behaviour of individuals in reality.

It is difficult to translate individual behaviours into a consistent formalism of equations, while agent based models support a more direct description. This generates an easier possibility to translate the findings of agent based models into practice. From this perspective agent based models have more the character of a “What if” study.

Depending on the research question the main disadvantage of equation based models in their application to behavioural science is the assumption of a homogeneous individual behaviour. The behaviour of individuals in real systems are often highly heterogeneous. This is not a necessary simplification in equation based models, but without it they get much more complex.

Wilson (1998) used a predator-prey system to compare both methods. He shows, that the application of ABM is the more realistic method. The disadvantages of equation based models in this example result from the use of averages of critical system variables over time and space. But when the dynamics are non-linear, small local variations from the average can lead to significant deviations in overall system behaviour (Hilborn, 2004). By contrast agent based models work inherently locally. Each agent monitors the value of system variables locally without averaging them over time and space.

### **4.2.3 ABM in life science**

There are two important criteria for validating an agent based model. They are the same for validating any model in science:

1. Does the behaviour of the agent-based model match the behaviour of the target system within the standard metrics of scientific evaluation?
2. Are all the attributes of the agents and their environment of the agent-based model characteristics the target system also possesses?

Considering scientific evaluation, these “standard criteria” depend largely on the success of previous explanatory efforts. If no one has generated a prior explanation or model, then it may be sufficient to show a qualitative similarity between the model and the target system. However, if there is another competing model, then it is necessary to use standard statistical hypothesis testing to see which is the better match (Bryson et al., 2007).

For the second criterion, the issue is whether the modeller has given the artificial agents any capacities that real subjects could not or arguably would not possess. For example, if we tried to explain the origins of theory of mind by using artificial agents that actually had perfect access to each other’s internal state, then we may have simply modelled the presumed end state of the system while providing no explanation for how that capacity came to be. However such a model might be useful if the true end state of the system was in doubt. For example, we might show that our “perfect knowledge” theory-of-mind agents were actually less socially capable than agents with imperfect knowledge. This might lead us to change some of our assumptions, e.g. from believing more social agents must be more perceptive, to some other explanation, such as more social agents require a higher capacity for propagating social norms.

#### 4.2.4 Analysis of agent based models

The analysis of agent based models should consist of three phases. The first phase is the *replication* of the agent-based model. This may not seem (or even be) strictly necessary if the model is publicly available – the results in that case can be checked just by rerunning the model on another computer. However, *re-implementing* the model from its description in the literature can be a valuable exercise, and may uncover important aspects of the model that the model’s original authors either took for granted, overlooked or even forgot about during the course of their research (Axtell et al., 1996). An agent based model may be valid without actually having been fully verified or understood. This is true of any scientific hypothesis; part of the scientific method is improving this understanding of a theory as a community (Bryson et al., 2007).

Once the critical attributes of the model are well understood, we can enter the second phase of the agent based model analysis, *model understanding*. Here it

is necessary consider carefully what the implied or the explicit correlates of its attributes are. Again, just as in any other scientific field, we go through a process of finding testable predictions and implications that result from our hypothesis.

The third and final phase is *testing* these predictions and implications, looking first into the existing literature, and then (if necessary) propose and execute new experiments.

Goodness of fit to data is by itself not a sufficient criteria for evaluating models as discussed earlier in this chapter. Computer science has shown that for large classes of computation there are an infinite number of mechanisms for achieving results that are all fundamentally equivalent (Turing, 1936). In natural science, when we have two models that make equivalent predictions we favour the simplest following the principle of parsimony (see section 10). Of course, when predictions are not precisely equivalent, trade off factors such as goodness of fit, simplicity and the capacity for generalisation can actually be quite complicated (Myung et al., 2000).

Modelling follows like other theory building processes the principle of parsimony. Complex individual behaviour is difficult to program, takes a long time to execute in simulation, and is difficult to analyse. There is therefore a strong bias towards looking for simple solutions. Our understanding of evolution to some extent justifies the assumption that the simplest solution that achieves an adaptive purpose is the most probable, because it is the most likely to be maintained genetically over time.

### 4.3 *NetLogo* in this thesis

In order to build a working model and make it easy to use for social scientists it was necessary to search for a suitable environment for implementing the new model. Such an integrated development environment (hereafter IDE) enables the development of different types of software. It usually includes a source code editor, a compiler and debugging tools. The aim was to find an environment that enables researchers to easily implement their theories while fully using the advantages of ABM.

After initially experimenting with *eclipse* as IDE and using python as programming language, it became obvious that this approach was not leading to the aimed for “easy to use” tool for the implementation and analysis of theories from social science. After searching for a more suitable tool for the task *NetLogo* was chosen. It is designed especially for modelling complex natural and social phenomena and complex systems developing over time. On one hand it is simple enough for programming rookies to implement their own models on the other hand it is advanced enough to be used in many research fields (Wilensky, 1999).

*NetLogo* is fully programmable and contains a graphical user interface (GUI) which enables the user to monitor agent movement and the development of results over time. Figure 4.1 shows a screenshot of the *Netlogo* GUI during a running experiment. In the centre the environment display with the agents (represented as differently coloured dots) is visible. It is surrounded by graphs which map the development of different variables during the experiment. The bars on the lower left hand side represent sliders for different experimental parameters which make an adjustment of these parameters according to the research question possible.

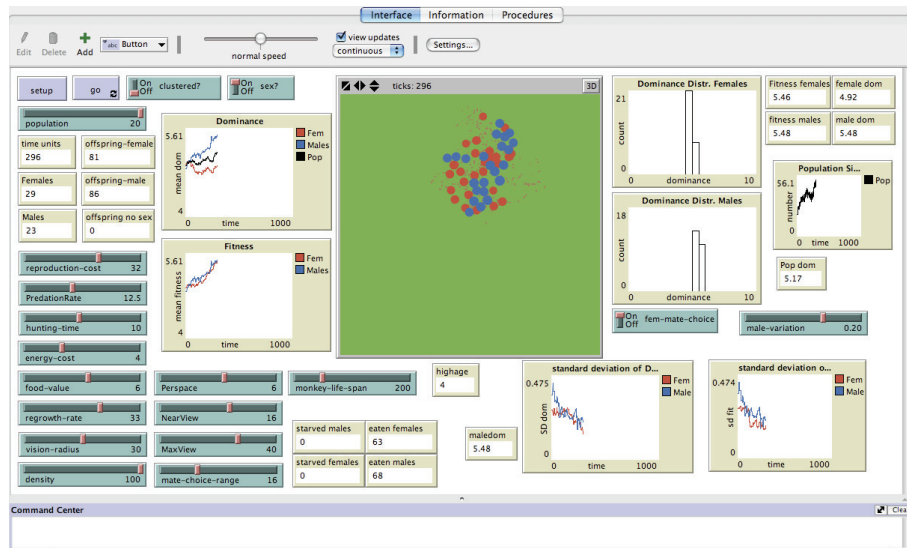


Figure 4.1: Screenshot of the NetLogo GUI

*Netlogo* also contains a tool called *BehaviourSpace*. The *BehaviourSpace* enables researchers to design and run different experimental setting with the model. With the *BehaviourSpace* it is also possible to easily run parameter sweeps in order to find the optimal configuration for planned experiments. This is another big advantage of *NetLogo* and also of ABM in general. This and its intuitive structure makes *NetLogo* a good environment to implement agent based models with soci-



ological research background.

## 4.4 Summary

ABM is a computer based modelling technique which enables researches to build individual agents and examine the effects of their interactions. The difference compared to conventional population based modelling, in which all agents in a population are the same, is the difference in the states of the variables describing each agent.

ABM will be used in the *NetLogo* environment in this thesis to model the social interaction patterns between individuals in different species of primates with different social structures. It has like any other theory building technique advantages and restrictions. Its biggest advantage is the ability to model interaction dynamics on an individual level, allowing the user to assign different traits to each agent and with that give each agent a different state under certain conditions. Its biggest restriction is the complexity of the theory to be modelled. Because each agent in an agent based model is different, the interpretability of effects added variables have on the interactions between the agents decreases with the number of added variables. In order to counter this problem it is useful to start with a simple model and then expand it by adding different factors to it.

# Chapter 5

## *DomWorld* and its replication

### 5.1 Introduction

Hemelrijk's work (Hemelrijk, 1999b,a, 2000, 2002a) represents one of the theories of primate social structure mentioned in chapter 3 which I wanted to examine. The facts that it is already specified as an agent based model and that it deals with primate social interactions are the reasons why I wanted to analyse her work first. Hemelrijk calls her modelling environment *DomWorld*. The code of her models however is publicly unavailable. This made it necessary to reconstruct her code based on information given in her articles. Most of the information about the dynamics of the interaction between the agents in her model is summed up in one repeatedly published flowchart (Figure 5.1) which served as foundation of the model discussed in this chapter.

At first an overview of *DomWorld* will be given and the process that lead to the replication of her results will be described. In addition to a critique of *DomWorld* and Hemelrijk's theory about the evolution of primate social structure this chapter includes also a description and critical analysis of several *DomWorld* experiments, conducted with this replication of *DomWorld*.

The version of *DomWorld* which was replicated deals with dominance structures in general, but focuses specifically on dominance interactions between males and females within a primate group. The model consists of small groups of agents

(representing male and female primates) situated in more or less close proximity to each other and interacting in different ways with each other. A result of how she implemented the interaction dynamics in *DomWorld* is that the dominance hierarchy of her agents is very dynamic and that the position of an animal in its group is very flexible.

This means that the rank of an agent during a simulation changes constantly depending on the outcome of the dominance interactions the agent is involved in. The frequency and outcome of these dominance interactions is based on the rank males and females have in the hierarchy of the group. This rank is determined by a variable called *dominance value*. The agent with the higher dominance value has the higher rank in the hierarchy of the group. The result of a dominance interaction is a change of the dominance values and therefore of the rank in the hierarchy of the group of the agents involved. The winner gains dominance value and the defeated loses dominance value.

After re-implementing *DomWorld* Hemelrijk's results were replicated successfully (Lehmann et al., 2005). Particular attention was paid to her explanation of the increase of dominance experienced by females during *tumescence*. Conducting these experiments, which aimed to explain the reasons for the transition of egalitarian social structure into a more despotic social structure, also made the testing of the validity of Hemelrijk's model possible.

## 5.2 Theoretical Background

As described in detail in chapter 3 most primate species are highly social. They live in structured societies with more or less steep dominance hierarchies. In steep dominance hierarchies individuals would never consider violating rank (e.g. a lower-ranked individual would not take food in the presence of a higher ranked individual). In groups with a less steep hierarchy, dominant animals show more tolerance towards subordinate behaviour, and consideration of rank plays a less important role in ordinary action selection. The differences between these social structures have been studied extensively in the different species of the genus *macaca* (Thierry, 1985, 1986b, 1990, 1994). Species with steep dominance hierarchies are often called *despotic*, while those with the less rigid dominance struc-

tures are called *egalitarian*. If a dominant animal allows a subordinate animal to take advantage of resources in its presence, the dominant animal is considered to express *tolerance*.

Tolerance is considered to be one of the basic forms of conflict resolution (de Waal, 1989). It is difficult to describe tolerance as an action an agent can select from its behavioural repertoire since it is more a decision not to act in the presence of a subordinate member the group. In some species, for example, this is achieved by the deliberate averting of gaze or by moving away from a resource in order to avoid witnessing a desired event, such as allowing a juvenile throwing a tantrum to gain access to food.

According to Hemelrijk, primate males are usually dominant over females, due to their bigger size, strength and higher level of aggression (Hemelrijk, 2002a). However, during the sexually attractive period of the females (*tumescence*), chimpanzee males for example, allow females priority in food access (Yerkes, 1940). This has been explained as a cognitive strategy (Yerkes, 1939) - an exchange of food for copulation (Goodall, 1986; de Waal and Luttrell, 1989; Stanford, 1996). Hemelrijk and her colleagues have proposed a cognitively-minimalistic explanation of this change in behaviour. Hemelrijk claims that there is no statistical evidence for such exchanges for food (Hemelrijk et al., 1992), neither is there any increase in sired offspring (Hemelrijk et al., 1999). One of Hemelrijk's model conditions produces results which show that a change in dominance can occur in despotic societies even without any benefit for the males, but as a simple consequence of the higher frequency of dominance interactions between the sexes due to increased attraction of the males to the females (Hemelrijk, 2002a).

In *DomWorld* in some conditions males are more tolerant towards females than in others. Male tolerance is measured as the number of females outranking males in the group hierarchy. In the model it is more likely that females outrank males in conditions in which their attractiveness is increased. Females are modelled as initially 50% weaker than males, and are always 20% less aggressive. Once an animal achieves a high rank, its strength increases accordingly to its new rank. The change of rank is determined by the outcome of the dominance interactions between the individuals. These dominance interactions take place between all the individuals in the group. It can therefore happen that a very low ranking individual has a dominance interaction with a very dominant individual. There

is also the possibility for this low ranking individual to win this interaction and become at once very dominant itself. This is questionable in terms of ecological validity (Bryson et al., 2007).

Hemelrijk explains her findings as a side effect of the higher interaction frequency between males and females. Normally animals tend to avoid invading each other's "personal space" and triggering a conflict, unless they have a higher rank than their opponent. However, in the experimental condition with female sexual attraction male agents ignore the rank of female agents. Due to the structure of Hemelrijk's dominance interaction algorithm it is possible that even very low ranking animals have a statistical chance of winning a fight with a dominant individual which can lead to an increase in rank. Another assumption of the model which is not entirely supported by empirical data are the constantly changing dominance values and the extremely flexible social hierarchy. Especially in primate species with a despotic social structure hierarchies are relatively stable over long periods of time. Even in species with a more egalitarian social structure a complete overthrow usually happens only after a relatively long time.

### 5.3 The *DomWorld* environment

*DomWorld* consists of a small group of agents located in more or less close proximity to each other, occasionally having aggressive interactions, which result in shifts of rank in the dominance hierarchy of the group. After running the model under different conditions quantitative descriptions of the agents' relationships such as the steepness of the dominance hierarchy are taken.

The replication of *DomWorld* was mainly based on the simulation described by (Hemelrijk, 2002a). The original version of *DomWorld* was written in Borland Pascal 7.0. The replication was written in NetLogo 2.1 because, as a purpose-built modelling tool, it provides a relatively easy high-level language for quickly constructing models and visualising the simulation and the results (see section 4.3). The model world resembles the geometrical structure of a torus. This avoids border effects and enables the agents to move in every direction. As described by Hemelrijk the model environment is 200 x 200 units. In the beginning of the simulation the agents are set at random locations within a 30 x 30 parcel in the

centre of the model environment.

The movements and interactions of the agents are determined by different parameters:

- Vision-angle = 120 degrees  
The agents “see” other agents which are in an angle of 60 degrees to either side of their direction of forward motion
- Comfort-distance (*NearView*) = 24 patches  
Agents maintain their activities as long as other agents are within this distance and within their vision angle.
- Maximum-group-distance (*MaxView*) = 50 patches  
If there is no other agent in *NearView* the agents check this distance and if they find another agent within this distance they turn towards it and move forward until this agent is in comfort distance
- Personal-space (*PerSpace*) = 2 patches  
If agents penetrate each others personal space they will engage in a dominance interaction.
- Search-angle = 90 degrees  
If an agent finds no other agent inside its Vision-angle and its *MaxView* it starts to turn 90 degrees to the left and to the right until it finds another agent.

After completing an action every agent is assigned a random waiting period before it can perform its next action. This is to simulate resting. In the model it means that agents do not engage constantly in dominance interactions. The waiting period is stopped if an agent observes a dominance interaction within its *NearView* during this period (Hemelrijk, 2002a, p.732). This matches empirical data which shows that in primate groups nearby fights are likely to trigger active behaviour (Galef, 1988).

The period of female receptiveness, in which the females are especially attractive to males, is in non-human primates called tumescence. In the model tumescence is operationalised as a variable called *attraction*. In order to test the effect of

tumescence the attraction in the model could either be switched off or switched on.

## 5.4 Structure of agent interaction

The interaction procedures in the model can be categorised into grouping interactions and dominance interactions. The grouping interactions represent the cohesive force which holds the group together and the dominance interactions represent the aversive force which drives them apart (Reynolds, 1987).

Hemelrijk (2002a) describes four interaction rules:

1. An agent observing another agent within its personal space may engage in a dominance interaction with it, depending on its own rank and the rank of the other agent. For such an interaction to take place, first the closest potential opponent is chosen. Then a procedure called *mental battle* is executed. This *mental battle* is similar to the actual dominance interaction by which it is succeeded (see eq. 5.1, page 68). The difference between the two is that the outcome of the *mental battle* only determines whether the agents engage in a dominance interaction or not. It has no influence on the dominance values of the engaged agents. The outcome of the dominance interaction on the other hand changes the dominance value of the agents. The winner gains dominance and the loser loses dominance. The size of the increase or decrease of dominance is determined by equation 5.3 (page 69). After such an interaction, the winning agent moves towards its opponent, while the loser turns 180 degrees and moves away.
2. If an agent detects no other agent within its personal space, but within its *NearView*, it then – in conditions without female attraction – moves one unit forward on its present course. In conditions with female attraction male agents change direction and move towards female agents they “detect” in their *Near View*. If the males see more than one female, they will move towards the closest.
3. If an agent detects no other agents within its *NearView*, but does detect one within its *MaxView* range it changes its direction toward its closest





sonal distance and the rank of the opponent is lower or equal to their own rank. The agent “estimates” its chances of winning by running a simulated fight (called *mental battle*) (Hemelrijk, 2002a). If it wins this *mental battle*, it starts the real fight (the chances of winning increase with the rank of the individual). The algorithm for this interaction is shown in equation 5.1. The dominance values for all males are equal in the beginning of each experimental run and initially the males outrank the females. The outcome of every single interaction influences the chances of winning the next one. Such a self-reinforcing system can be found in many animal species (Hemelrijk et al., 2008).

The algorithm for determining the outcome of a dominance interaction was taken from Hogeweg (1988) (Hemelrijk, 1999b, 2002b). Each agent has a certain dominance value determining its position in the hierarchy of the group. This dominance value is readjusted according to the outcome of every dominance interaction an agent is involved in. Hemelrijk calls this representation of dominance *Dom-value* (Hemelrijk, 2002a). This *Dom-value* is correlated both to the agent’s rank and its ability to be successful in an interaction. The outcome of a dominance interaction is calculated by the following algorithm (from Hemelrijk, 2002b, p. 734):

$$w_i = \begin{cases} 1 & \frac{Dom_i}{Dom_i + Dom_j} > Random(0, 1) \\ 0 & else \end{cases} \quad (5.1)$$

Random(0,1) produces a random real value between 0 and 1.

In this algorithm  $w_i$  is the value which determines whether agent  $i$  has lost or won. 1 represents victory and 0 defeat. The relative dominance value is compared with a random number between 0 and 1. If the dominance value is bigger than the random number, the agent wins. As a result an agent is more likely to win an interaction if its rank is higher compared to the rank of its opponent, but a very low ranking agent still has a small chance to win. After a dominance interaction, the *Dom-Values* of both agents are changed according to the outcome. If an agent wins, its *Dom-Value* increases. If it loses, its *Dom-Value* is lowered. The new dominance values of the agents are calculated according to equation 5.2. The lowest *Dom-Value* an agent can have is 0.01. This is to prevent negative *Dom-Values*.

$$\begin{aligned}
Dom_i &= Dom_i + \left( w_i - \frac{Dom_i}{Dom_i + Dom_j} \right) * StepDom \\
Dom_j &= Dom_j - \left( w_i - \frac{Dom_i}{Dom_i + Dom_j} \right) * StepDom
\end{aligned} \tag{5.2}$$

Hemelrijk calls this system for adjusting dominance values according to a dominance interaction *damped positive feedback system*. In case of winning the dominance value of a high ranking agent advances only slightly, but if a low ranking agent wins its dominance value increases largely. This is supposed to reflect the fact that it is very unlikely for a low ranking individual to win a dominance interaction with a high ranking member of its group. But it is questionable in terms of ecological validity and has been criticised repeatedly (Bryson et al., 2007; Lehmann et al., 2005).

The extent of rank shift is largely affected by *StepDom*. This variable represents, according to Hemelrijk (1999b), the intensity of aggression displayed during a dominance interaction. High levels of *StepDom* represent the type of aggression exhibited in “despotic” species, and low levels of *StepDom* represent the type of aggression exhibited in “egalitarian” species. The value for *StepDom* is set in the beginning of each simulation and ranges from 0 to 1 with an increment of 0.1. With a high *StepDom* value the changes in the dominance value after an interaction are big, with small *StepDom* value they are small. Even though in Hemelrijk’s models *StepDom* represents aggression, it has no direct impact on the outcome of the dominance interaction (see eq. 5.1), but it has a long-term impact on the dominance values and therefore on the probability of each single agent to win or to loose possible future interaction.

An important measure in DomWorld is the *coefficient of variation of dominance values*. It represents the average variation between the different dominance values of the individuals in the group. A high coefficient of dominance variation indicates large differences between the ranks in the hierarchy. This is typical for despotic primates species (Thierry, 2004, 2006). They are characterised by a ‘steep’ and unambiguous dominance hierarchy with great differentiation in rank. The opposite is true for egalitarian species. They are characterised as having relatively ambiguous rankings. In the model this would be represented by a low coefficient of dominance variation.

According to the structure of the interaction algorithm of Hemelrijk’s model there isn’t a qualitative difference between despotic and egalitarian primate species in terms of the way subordinate individuals treat dominant individuals. In her model every agent shows an equal amount of respect towards a member of its group with twice of its dominance value.

## 5.5 Experimental Set-Up

In order to replicate the results from Hemelrijk (2002a) the parameter settings described in Hemelrijk (1999a, 2000, 2002a) were used. Each group contained 8 agents ( $N = 8$ ), four males and four females. Each agent had a personal space of 2 ( $PerSpace = 2$ ), a vision angle of 120 degrees, a maximum-group-distance of 50 units ( $MaxView = 50$ ) and a comfort distance of 24 units ( $NearView = 24$ ). The search angle was 90 degrees, the fleeing distance was 2 units ( $fleeD = 2$ ), the fleeing angle was 45 degrees at random direction away from the opponent and the chasing distance was 1 unit ( $chase = 1$ ) in the direction of the opponent. To resemble the difference in physical strength between males and females both sexes started out with different *DomValues* ( $female\ agent = 8$ ,  $male\ agent = 16$ ). Females had only 80% of the aggression intensity (*StepDom*) of males.

Variable	Setting
attraction	on or of
intensity of aggression	0.1 or 1
population 8	20 or 60
chasing distance	1
fleeing distance	2
initial dominance of females	8
initial dominance of males	16
Perspace	2
NearView	24
Max-View	50

Table 5.1: Initial parameter settings for the DomWorld replication model

Experiments were conducted under 4 different conditions. Two levels of aggression were used in which the sexual attraction of the females was either switched on or off. In the despotic condition with high aggression, male *StepDom* was 1 and females *StepDom* was 0.8, in the egalitarian condition with low aggression, male *StepDom* was 0.1 and females *StepDom* was 0.08. The experimental runs for each of the conditions were repeated 10 times, resulting in a total number of 40 runs.

## 5.6 Results

The data was analysed in the same way Hemelrijk (2002a) describes it. The results of the replication match her results. Figure 5.2 (pg. 72) shows the mean number of male agents ranking below female agents during the simulations in different conditions. As reported in Hemelrijk (2002b) the number of male agents having a lower dominance value compared to female agents increases over time in conditions with female attraction. In the condition with high aggression and female attraction the number of subordinate males is biggest. In conditions with low levels of aggression none of the male agents become subordinate to female agents.

Figure 5.3 (pg. 73) shows the classic Hemelrijk result. It shows the distribution of the *coefficient of dominance variation* of dominance values for both male and female agents. This coefficient is a measure for the steepness of the group hierarchy. The bigger the coefficient is the bigger are the distances between the ranks in the group hierarchy. In conditions with high levels of aggression, the coefficient is steeper than in conditions with low levels of aggression. Attraction as additional variable amplifies this result. The bigger difference between the conditions with low and high levels of aggression suggests that aggression is the main factor.

Figure 5.4 (pg. 74) shows the distribution of dominance values for male and female agents in conditions with high and with low levels of aggression. In conditions with high levels of aggression the dominance structure is changing constantly and the differentiation of ranks in the hierarchy is bigger. Female agents can in these conditions outrank male agents. In conditions with low levels of

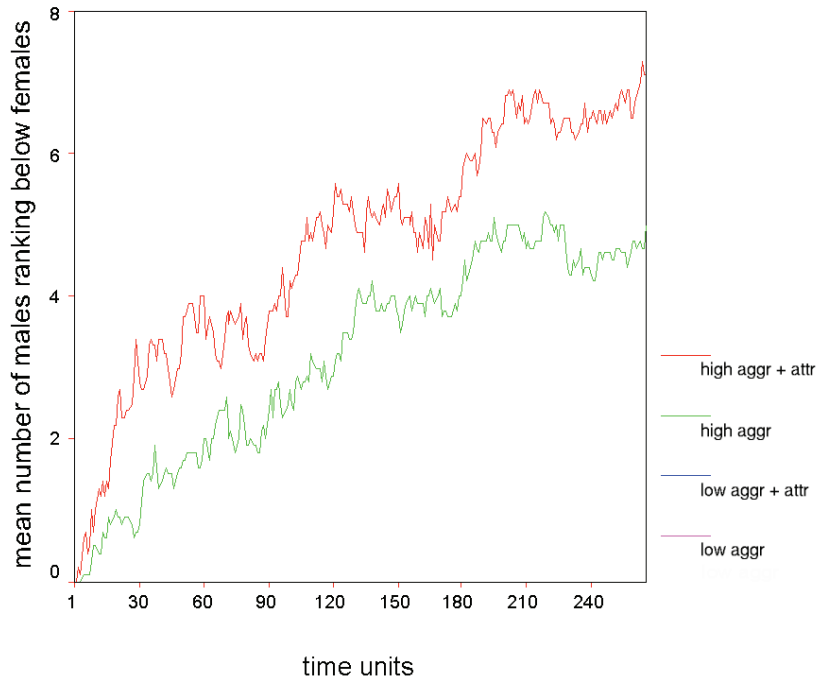


Figure 5.2: Mean number of male agents ranking below female agents in different conditions. Replication of Hemelrijk (2002a, Figure 3A, p.739). For both conditions with low aggression the number is 0.

aggression the distribution of dominance values changes only a little creating a stable hierarchy structure. Females never outrank males in these conditions.

Figure 5.5 (pg. 75) shows the total number of dominance interactions initiated by female agents in all four different conditions. It shows that the number of dominance interactions initiated by female agents increases in conditions with sexual attraction in both intensities of aggression (Mann-Whitney,  $N = 10$ ,  $U = 0$ ,  $p < .001$ , two-tailed, Mann-Whitney,  $N = 10$ ,  $U = 0$ ,  $p < .001$ , two-tailed). Female agents are therefore involved in significantly more dominance interactions if they are attractive. A higher level of StepDom amplifies the result.

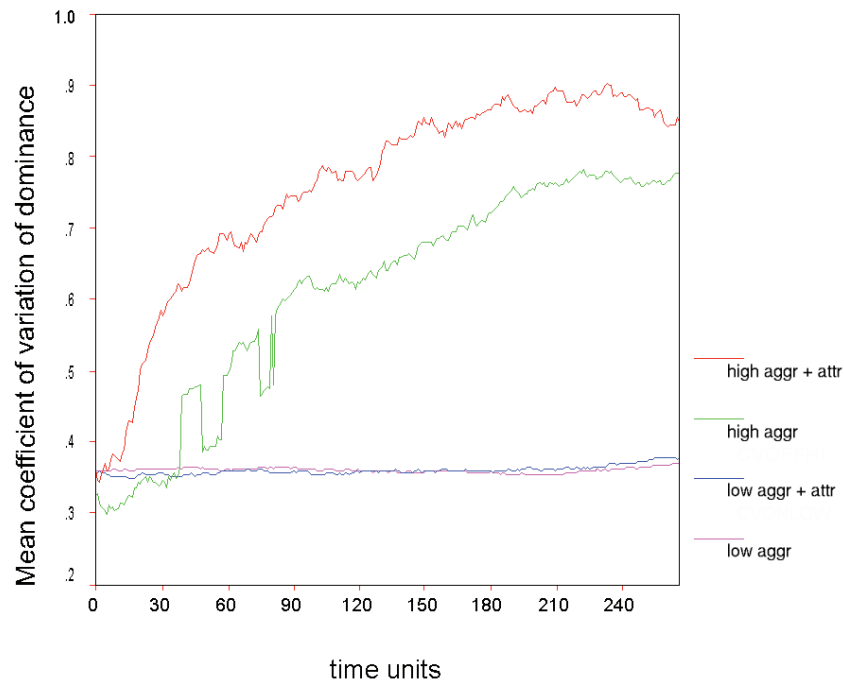


Figure 5.3: Coefficient of dominance variation in different conditions for all agents. Replication of Hemelrijk (2002a, Figure 4A, p.741)

## 5.7 Discussion

### 5.7.1 Results from Hemelrijk's model

The results show the same structure as the results in the original study (Hemelrijk, 2002a). The replication can therefore be considered as successful. In general there are four different results deriving from this model. Since these results have already been described by Hemelrijk in various papers only a brief overview will be given at this point.

- The differentiation of dominance values increases in conditions with high levels of aggression. In conditions with low levels of aggression the differentiation is only marginal. In terms of the model this means in conditions with high aggression the hierarchy of the group is more flexible enabling individuals to gain or loose rank in the group easily. On the other hand in conditions with low aggression the results show that it is very unlikely for

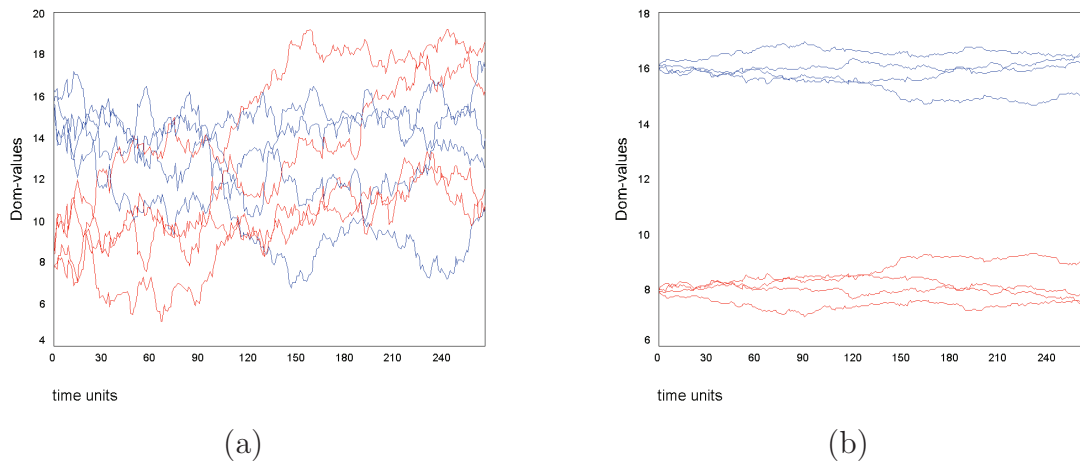


Figure 5.4: Distribution of dominance values in conditions with a high levels (a) and in conditions with low levels (b) of aggression. Replication of Hemelrijk (2002a, Figure 4B, 4C, p.739). The blue lines represent the dominance values of male agents and the red lines the dominance values of female agents.

single agents to change rank and become more dominant.

- The increase of female-initiated dominance interactions depends more strongly on female attraction than on increased levels of aggression. Due to the interaction structure and the increased probability of males approaching females, the overall number of interactions females are involved in increases, giving them a bigger chance to increase their dominance value.
- Only conditions with high levels of aggression females are able outrank males. If additionally to this females are sexual attractive this effect is amplified. This means, according to Hemelrijk's model, if in a group with high levels of aggression (despotic) females become sexually receptive, the probability of them gaining ranks in the group hierarchy increases, due to the fact that they become involved in dominance interactions more often. This connection between higher interaction frequency and relative dominance is proposed by Hemelrijk (2002b) as a parsimonious explanation for the observed male tolerance towards females in periods of female tumescence.
- The *coefficient of dominance variation* increases in conditions with high levels of aggression and reaches its highest value in conditions with a combination of high aggression and female attraction. Being a measure for the steepness of the hierarchy this means the distances between the different individual ranks are largest in conditions with high levels of aggression and

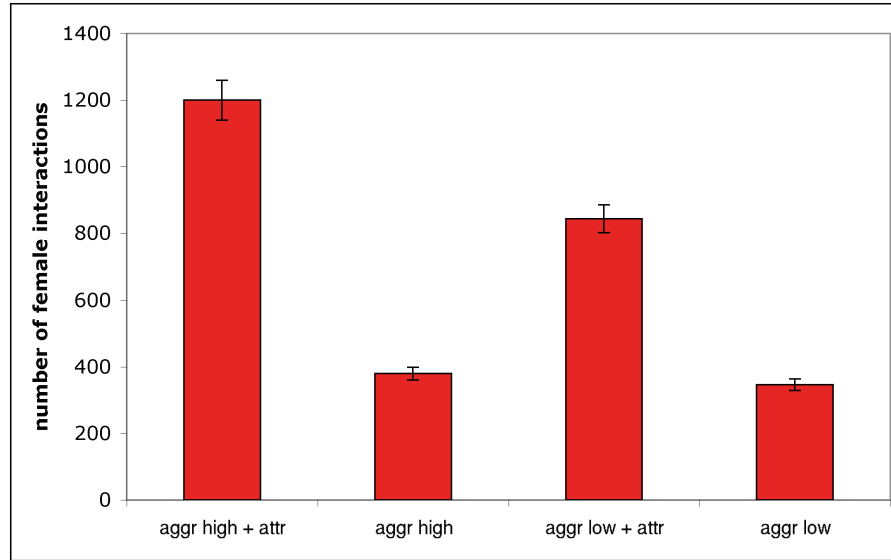


Figure 5.5: Number of dominance interactions initiated by female agents for the different experimental conditions (aggr high + attr = high aggression + attraction, aggr high = high aggression, aggr low + attr = low aggression + attraction, aggr low = low aggression) It is a replication of Hemelrijk (2002a, Figure 2B, p.737)

female attraction.

Hemelrijk’s model seems to be a good analogue system for macaque behaviour. *DomWorld* shows that apparently complex behaviours in primate societies like “male tolerance” or “female assertiveness” can be generated in agent based models with only a few simple assumptions about individual behaviour. The effect of female dominance appears for example in the conditions with high aggression and is consolidated by a high level of attractiveness in these females. This contrasts with the classical explanation of this phenomenon, which propose food for sex exchanges or hormonal regulated processes (Goodall, 1986). Hemelrijk’s model does not include any food, real sex or hormones and still leads to similar results.

Once having a working model, understanding exactly how these phenomena emerge is possible. Analysing what the critical factors of the model are, and looking for biological correlates that would either prove or disprove the model is the next step.



### 5.7.2 Approach to analyse Hemelrijk's theory

The results of DomWorld are based on two assumptions:

1. the self-reinforcing effect of dominance
2. the fact that females attract males in their time of tumescence

The first assumption relates to the fact that the dominance value of an individual (operationalised as the ability to win a fight) increases with a victory and decreases with a defeat. Although this self-reinforcement is a well-known phenomena that has been studied extensively in laboratory animals such as mice, the validity of the operationalisation of this phenomenon the way it is used in this model is unclear. In the model, the strength of the effect is determined by the dominance rank of the opponent, the 'level of aggression' (that is, the *StepDom* value assigned to this species) and chance. The result of a fight and the dominance level after a fight are calculated with equations 5.1 and 5.2 (page 68).

Hemelrijk has defined aggression as a variable called *StepDom*. Following the above mentioned equations an individual increases its ability to win a fight and thus increase its dominance most, if it wins against an individual with a preferably much higher dominance level and in conditions with high levels of aggression. But in natural setting subdominant individuals would not even try to get involved into dominance conflicts in these conditions. This makes the ecological validity of this approach problematic.

Aggression is therefore a crucial value which decides within the system how far an individual can go up or fall down in the hierarchy as the result of a single fight. This is the basis of the reinforcement effect of dominance. Hemelrijk et al. (2008) give a variety of examples for the effect in nature. Intuitively it might be plausible, that self-confidence about winning a fight increases in an individual, if it wins against someone much stronger and in adult mammals even growth hormones can be triggered by success in social competitions (Rutte et al., 2006). But nevertheless in a real fight it is highly unlikely to win against a much bigger and much more dominant individual, especially in species with a despotic social structure.

To test the validity of Hemelrijk’s first assumption, it is necessary to carefully examine any events documented in which a low ranking individual displaced a higher ranking individual of its group in a competitive interaction, and see how this influenced dominance structure of the group. The following factors are particularly important:

- If an agent defeats another agent vastly outranking it in a dominance interaction, do the two agents immediately switch their positions in the hierarchy of the group? In other words, is an unexpected outcome from a fight likely to have a significant effect? If yes, the use of relative dominance values in Equation 5.2 would be legitimate.
- Does it take fewer dominance interactions to advance in rank in groups with a more despotic social structure? If this is true, use of StepDom in Equation 5.2 would be justified.
- If a fight is more violent (e.g. if blood is drawn compared to mild beating), does it have more impact on the dominance hierarchy? If this is so, then it makes sense to refer to *StepDom* as aggression and it would further justify its use in Equation 5.2.
- Are females more likely to engage in fights when they are sexually receptive? If not then this model does not account for the tolerance shown by males towards them in such periods.
- Is the way two individuals, which are far apart in the dominance hierarchy of their group, engage in dominance interactions similar to the way two individuals which are closer together engage in the same type of interaction?

The answers to these questions would help to validate whether steepness of the dominance hierarchy is a good representation of despotic and egalitarian social structure.

It is also important to have a critical look at Hemelrijk’s second assumption, the idea that female primates attract male primates in their receptive period and that this leads to an increased number of dominance interactions which lead in turn to a higher probability of occasional lucky wins by females which immediately

catapults them up the dominance hierarchy. The question remains as to whether this is at all plausible.

The difficulty determining whether the assumptions of this model are valid is that the dominance hierarchy and the social structure of a group depend not only on the variables used in the model but also on other factors like food distribution and availability, predation pressure and inter-individual differences in physiology and personality. Some animals will behave differently with respect to others depending on what other animals are present in a situation (Harcourt, 1992). Many researchers work diligently to establish these sorts of records, so we can hope to find answers to these questions soon.

### 5.7.3 Critique of Hemelrijk's theory

The rules determining the resulting dominance of an individual after a dominance interaction cannot explain the change of male behaviour towards females during periods of female tumescence on their own. Even if males are more tolerant towards females, this doesn't mean females can gain higher ranks than adult males in groups in which they are subdominant outside of their sexually attractive period. The version of *DomWorld* replicated in this work might therefore be able to explain some of the inner group dynamics during periods of female tumescence, but it cannot account for permanent changes or the evolution of different stable social structures due to its extremely dynamic operationalisation of the dominance hierarchy. In order to do so, such a model needs additional factors to explain more sufficiently the variety of different phenomena connected to social behaviour and social structure. Also in Hemelrijk's model aggression is not costly for the agent. There are no negative consequences for an agent if it loses a fight. Since one of the possible reasons why hierarchical structures in social groups have evolved is to minimise the risk of injury after an aggressive interaction it seems very implausible not to implement aggression costs into the interaction dynamics of the model.

Another important point is the lack of empirical data on subordinate individuals beating dominant individuals in a direct confrontation in species with a despotic social structure, suggesting that this is not very common. In the model low-ranking females can outrank very dominant males only in the condition with a

high level of aggression, which represents a despotic social structure. The results and dynamics of the model are based on this effect. It can therefore not explain the evolution of despotic and egalitarian social structures.

## 5.8 Conclusions and Discussion

One problem of replicating Hemelrijk's model was that there is no actual code available online. The entire model needed to be reconstructed from information gathered from various articles. The code of the replication however was made available for every researcher who wants to work with it and possibly improve it. In my opinion it is important, if we want to work with ABM in social science, not to be afraid to openly discuss the code the models are constructed of. It helps to improve the quality of the models and is a fast way to test the theories the models are based on.

By matching the results of Hemelrijk (2002a) this replication can be considered successful. In the process of implementing *DomWorld* from the information given in different papers, some discrepancies became evident (e.g. a very dynamic hierarchy structure) which made the ecological validity of different factors the model is based on controversial.

From this replication there are two possible ways to pursue the search for the answer of my research questions. First I wanted to see which environmental constraints make dominance beneficial to the individual or group and second what accounts for the differences in primate social structure. For both questions it is necessary to integrate environmental factors into the model. Based on the theoretical background a good starting point for the extension of Hemelrijk's model is the integration of food and predation. Also in order to test the adaptiveness of dominance over time, it is necessary to integrate a reproduction mechanism.

Even though the replication of *DomWorld* has led to criticism, such as the very dynamic social hierarchy, the lack of costs for aggression, the undifferentiated way the agents engage in dominance interactions in conditions with different levels of aggression and the lack of empirical evidence for subdominant individuals gaining a high position in the group hierarchy by winning against a very dominant

individual in the group, it was the starting point for the other models presented in this dissertation. The first part of Hemelrijk's dominance interaction algorithm, the so called "mental battle" is a good representation of how the anticipation of a possible win or loss of a confrontation by an animal might work. This and the dominance interaction, with exception of the changes of dominance value after the interaction, were used in the other models in this thesis in order to simulate displacement behaviour. Generally speaking the *DomWorld* experience helped to understand the problems of agent based modelling better. It helped to understand that a good operationalisation of the variables the model depends on is crucial for its validity.

In the next step I modelled and attempted to validate the socio-ecological theory. First I constructed a simpler model dealing with the adaptiveness of dominance. It is called *Dominance Inheritance Model* and is based on basic assumptions of Hamilton (1971) on group formation. Starting from a few basic assumptions and then adding complexity to a model step by step helps to understand the dynamics of the model and its results. In the next chapter the first version of the *Dominance Inheritance Model* will be discussed.

# Chapter 6

## Possible reasons for the evolution of social dominance

### 6.1 Introduction

In this chapter a model is presented which aims to test whether predation pressure could be seen as the initial reason for the evolution of dominance related traits like the ability to displace other individuals in a group. Since the effects of this model are based on the transmission of dominance values from one agent generation to the next, it is called **Dominance Inheritance Model** (hereafter DIM). As mentioned in chapter 2 there is a qualitative difference between mere agglomerations of animals and social groups. The complex social behaviour exhibited in social groups is probably a relatively late adaptation to the group situation. But how did the evolutionary process towards complex social structures start? A possible answer is that it was initialised by a selection towards dominance behaviour based on displacement ability.

It is very likely that it was more efficient to forage in groups and that the group situation provided more safety for single individuals (Hamilton, 1971; van Schaik, 1983). Predatory species very soon could have adapted to this new situation by evolving stalking techniques and attacking individuals on the fringes of these agglomerations of individuals. A result of this process is that the space in the centre of a group becomes a valuable resource providing higher chances to reproduce for

individuals occupying it. In a scenario like this it is advantageous to be able to displace others. This could be a parsimonious explanation for the evolution of dominance structures.

Different traits are imaginable as source for the ability to displace conspecifics. Body size and with it physical strength is the first thing that comes to mind. But body size as main source for social dominance has very strict limits. An individual which is compared to its conspecifics larger needs to feed longer and to more in order to maintain its energy level and defend its position. The costs of increasing body size is therefore the time the individual has to spent in order to get its food. This restriction combined with the limitation of food due to group foraging leads possibly to other more complex ways of gaining social dominance.

The DIM tests the general effect of predation pressure and restricted food availability on the development of a variable called dominance value in an agent population. The social interactions between the individuals of this group are based on a displacement algorithm. The exact definition of the algorithm and what is meant by dominance value is given in section 5.4. The first set of experiments tests the influence of the two above mentioned environmental factors on the development of the average dominance value in the group. In the second set the effect of the displacement algorithm itself on the dominance value development in the group will be tested. The DIM will also serve as starting point for the extensions and experiments presented in the next chapters.

## 6.2 Background

The DIM tests why social dominance could have become adaptive. Its results represent a possible parsimonious explanation for the existence of social dominance. They are based on displacement behaviour and spatial location of individuals within a group and not on higher cognitive functions. If dominance based on displacement behaviour is one of the decisive traits separating agglomerations of animals from social groups this explanation might be sufficient.

The central parts of this model are the inheritance algorithm and the two basic principles of group formation, cohesion and repulsion. The repulsive force in

the model is the displacement behaviour of the agents. In order to model this behaviour the model uses the first part of the DomWorld interaction algorithm (Hogeweg, 1988; Hemelrijk, 1999b), the so called mental battle (discussed in section 5.4). If individuals come in close proximity to each other they compare their dominance values. After this comparison the individual with the higher dominance value displaces the other. The subordinate flees away from the dominant and the dominant takes its place.

The main difference between DomWorld and the dominance inheritance model is the way the agents interact with each other. In DomWorld the result of a fight changes the dominance value of the agents involved. This results in a highly dynamic social structure. The highly dynamic social hierarchy is one of the critical points in Hemelrijk’s models (Lehmann et al., 2005). It was avoided in this model by only using the “mental battle” of her interaction algorithm. The agents only displace each other after an interaction. Other differences are that the agents grow old and die, have offspring and that the offspring inherits traits from the parent. This allows to ask different questions than with DomWorld, although parts of DomWorld were modified and used in this model.

The cohesive force in the natural grouping process is the “urge” of the individuals to stay together, which is the ultimate effect of predation avoidance (Hamilton, 1971). In the model this “urge” is determined by different vision parameters. If an agent moves too far away from all other members of its group, it stops and starts to search for the direction in which most of the other members of its group are located and then moves in this direction until it is within a certain range of its conspecifics. This behaviour is comparable with the grouping behaviour observed in gregarious animals. Even if there is no immediate threat by a predator, the animals have an estimate of the risk level in their environment (Zuberbühler and Jenny, 2002) and group according to it.

## 6.3 Methods

The model world has the shape of a torus with a size of 240 x 240 patches. A patch is a squared raster element representing a spatial unit of the environment. At the beginning of each simulation every patch has a energy-value assigned to



it and is therefore classified as food patch. The status of a patch changes if an agent moves over it. If this happens the energy value of the patch changes to zero and stays zero until a certain number of time steps (*regrowth time*) have passed.

Predation during the simulation is statistical. After a predefined time interval a certain number of agents get killed. This number depends on a variable called *PredationRate*. The use of statistical predation was the easiest way to replicate the observed impact of a single predator on a population.

Nevertheless I have experimented with a predator breed and after doing various test runs I realised that the structure of the results would match the structure of the results of the more “simple” version. Integrating an additional breed of agents into an agent based model increases the complexity of the model to a large extent. As discussed in section 10 an increase in complexity is also always related to a more difficult interpretability of the results. The predators were implemented as a additional type of agents. They had vision variables in order to detect monkey agents in their surroundings. They also had an energy threshold which was reduced over time. If it dropped below a certain level the predators started to hunt, otherwise they waited until a potential prey would move close to them. A predator always killed its prey if the hunt was activated. Since the predators were outside the monkey group and always pursued the monkeys closest to them, the result was a stronger predation pressure on the monkeys at the fringe of the group. Since this effect could also be achieved more easily by integrating statistical predation it was decided to run the model without an actual breed of predator agents.

Based on the experience from the test runs with the predator breed the statistical predation works as follows: If the “hunt” is on, the position of each prey agent relative to the centre of its group is measured. Then the distance of the position of each agent from its local group centre is calculated. These distances are sorted and written into a list starting with the largest value. From this list a percentage of agents is killed. The percentage depends as mentioned above on the *PredationRate*. The agents killed are always the ones with the largest distance from the centre of their group. This procedure results in a higher probability for an agent to get killed by predation if it is on the fringe of its group (Hamilton, 1971).

The centre of the group of an agent is represented by the sum of the x-coordinates

of all other agents in its vision radius divided by their number and the sum of the y-coordinates of all other agents in its vision radius divided by their number. The vision radius of an agent represents the distance in which it considers other agents to be members of its group and is a predefined variable. This way of calculating the centre of a group also follows the idea of Hamilton (1971). As discussed in section 2.3 the safest place for an individual is to be as close as possible to a conspecific. Adding the x- and y-co-ordinates of all individuals in a certain radius and dividing them by the number of the individuals results in co-ordinates which characterise a point that is closest to all of these individuals.

### 6.3.1 Agents states and behaviours

The environment contains a group of agents representing a species of gregarious animals. Each of the agents has a repertoire of different behaviours from which it can choose how to interact with its environment according to its internal states. These behaviours are in the model sorted in a list. All the behaviours on this list are called every time step, but depending on the internal state of the agent only the behaviour which has priority in the moment is executed.

In order to be able to navigate in and interact meaningful with its environment an agent needs to have information about it. The agents in this model “know” where other agents of their group and food patches in their proximity are. Each agent has different vision variables assigned to it, a *maximum group distance*, a *comfort distance* and a *personal space*. The *maximum group distance* determines how far an agent can move away from the centre of its group. The comfort distance determines the range in which the agent feels safe in the group and can feed or move around depending on its internal states. The personal space is the immediate area surrounding the agent in which it does not accept any other agents. These parameters correspond to the parameters Hemelrijk used in her models (Hemelrijk, 1999b, 2000, 2002a).

The agents have a front and a back and therefore a direction in which they “look” while moving or interacting in the model environment. They also have a vision angle. They detect everything that is within their vision angle in the direction they are facing and in their vision radius. The vision radius determines how far an agent can “see”. Vision angle and vision radius are predefined variables.

The agents in the model can die of starvation, predation or old age. Each of the agents has an energy threshold which is reduced every step they move. In order to stay alive, the agents have to extract energy from the environment in such a way that they move over food patches. If the energy of an agent drops below a critical level the agent starts to “search” for the closest food patch within its vision angle and vision radius and moves towards it. If this food patch is too far away and the agent’s energy level drops down to zero before reaching it, the agent dies. Agents in the model also have a maximum life span after which they die. The length of the life span is a predefined variable.

In the beginning of the simulation each agent has a dominance value assigned to it. If an agent reproduces it passes its dominance value on to its offspring plus or minus a small random variation.

As described above the environment contains patches which either have an energy value assigned to it (food patches) or are empty. If an agent moves over a food patch, the energy value of the patch is added to the energy threshold of the agent. Once a patch has been emptied it stays empty for a predefined time period. Until the energy value of the patch is restored agents moving over it can’t extract energy from it. The food availability in the model is therefore determined by how fast the empty patches “re-grow” their energy values.

In this first version of the model the agents reproduce asexually. Sexual reproduction is added into the model and discussed in chapter 8. Asexual reproduction in the model means that every agent can on its own spawn an offspring once it has reached a certain energy level. In the case of this model the offspring inherits the dominance value of its parent plus or minus a small random variation. The new agent starts with a certain level of energy which is determined by a variable called *the reproduction costs*. This energy is subtracted from the energy of the parent and given to the child. The reproductive success of an agent depends on two factors. First on its predation avoidance ability and second on how fast the agent is able to obtain enough food in order to reach the energy level it needs to reproduce.

An agent executes behaviours based on its internal states. Besides the status of its energy level, these internal states are also determined by what the agent “senses”. If it senses other agents of its group in *comfort distance* it moves around

freely, feeds or reproduces. If it doesn't see other agents in this distance, it looks for agents within *maximum group distance*. If it sees agents in its *maximum group distance* it moves three steps towards them. If it doesn't see agents in this distance it moves towards the centre of its group until it sees other agents in *comfort distance*.

If an agent enters the *personal space* of another agent while moving around, a dominance interaction between the two agents encountering each other is triggered. During a dominance interaction both agents compare their dominance values. This comparison is similar to the mental battle in Hemelrijk's *DomWorld* (Hemelrijk, 1998; Hogeweg, 1988), but unlike DomWorld there is no fight and the dominance values of the opponents don't change after the interaction in order to maintain the relative positions of the agents in the dominance hierarchy. Depending on the result of the dominance interaction the agent with the higher dominance value displaces the other agent. The displacement works in such a way that the loser will flee a predefined distance away from its opponent.

The fleeing distance is twice as far as the chasing distance of the winner. In the second set of experiments in this chapter the fleeing distance and the chasing distance are varied in order to test the effect of the displacement mechanism.

### 6.3.2 Experimental Setup

Two different sets of experiments were conducted. In the first set of experiments the effect of displacement behaviour was tested. These tests were run with two different conditions. In the first condition the fleeing and the chasing distance were the same. This condition served as the control condition, so the configuration of the two environmental factors was chosen in such a way that they enabled a more or less stable average dominance value in the population. The problems with findings this configuration and with it one of the difficulties in ABM are discussed in more detail in section 6.5. In the second condition the fleeing distance of the subordinate agents was twice as far as the chasing distance of the dominant agents.

With the second set of experiments the effects of predation pressure and food availability in interaction with displacement behaviour on the development of

the average dominance value were tested. These tests were run with two different setups. In one setup the effect of different rates of predation pressure were tested in an environment with no food restrictions. In other words the effect of a relatively low and a relatively high predation rate on the average dominance value in the agent group was tested in an environment with a food availability of 100%. In the other setup the effect of different food availability rates on the average dominance value in the agent group was tested in an environment with no predation.

The experiments were repeated 50 times for each condition. Every run had a length of 5000 time steps, which corresponds to 50 generations in the model. The population started with a size of 20 individuals which were randomly distributed over an area of 20 x 20 patches in the middle of the environment. These setup-values as well as the values shown in figure 6.1 were chosen after numerous preliminary test runs with the model. They enable a stable running of the model. How the test runs were done and why they are necessary will be discussed in section 6.5. As results the development of the dominance values during the simulations was measured.

<b>Variable</b>	<b>Setting</b>
predation rate	10 or 15
initial population	20
hunting-time	10
reproduction costs	32
energy costs	4
foodvalue	6
regrowth-rate	45
agent life span	100
Perspace	6
NearView	16
MaxView	10

Table 6.1: Initial parameter settings for the dominance inheritance model

## 6.4 Results

### 6.4.1 Displacement

Figure 6.1 shows the development of the average dominance value in conditions with and without displacement. In the condition with displacement the average dominance within the population increased. The condition without displacement represents the control condition. Although the control condition was set to neutral selection, it shows in fact a slight decrease in the average dominance value. Nevertheless, the experimental condition shows significant increase of selection for dominance.

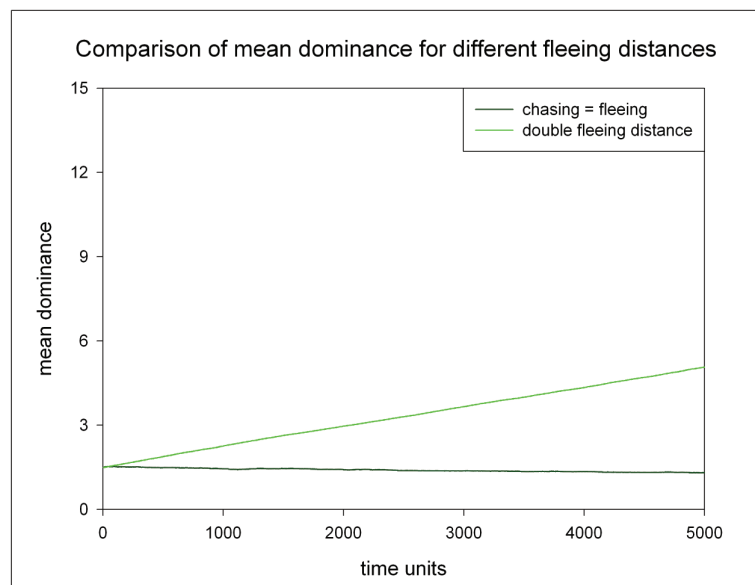


Figure 6.1: Development of dominance for conditions with more or less displacement

### 6.4.2 Predation pressure and food availability

Figure 6.2 shows the selective pressure for dominance in an environment with 100% food availability. It compares the average dominance values during the condition with a relatively high predation pressure with the average dominance during the condition with a relatively low predation pressure. In the condition with relatively high predation pressure the average dominance value increases

more than in the condition with relatively low predation pressure.

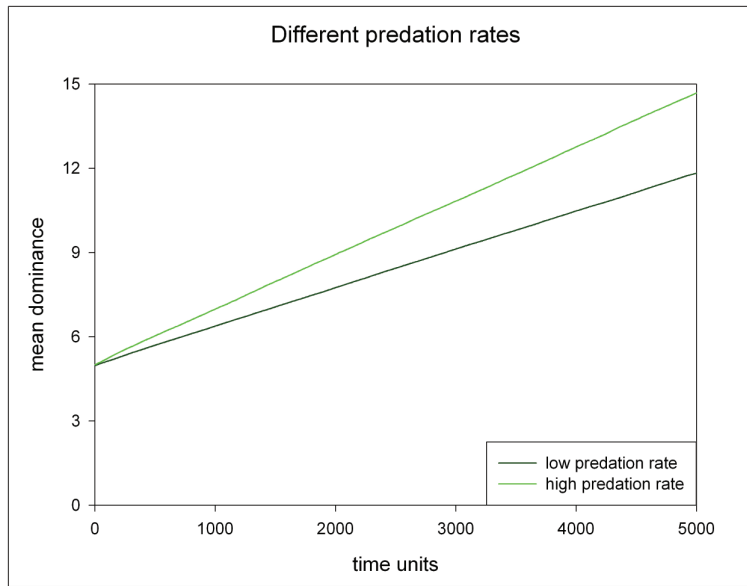


Figure 6.2: Development of average dominance for conditions with high or low rates of predation

Figure 6.3 shows the selective pressure against dominance in an environment with no predation. It compares the average dominance values during for the condition with relatively high food availability and with relatively low food availability. In the condition with relatively high food availability the average dominance value decreases more slowly compared to the dominance in an environment with relatively low food availability.

## 6.5 Discussion

The results of the model show that if dominance is based on the ability to displace other individuals, then predation pressure could be a possible reason for the selection towards dominance. The higher the predation pressure in the model environment is, the steeper is the increase of the average dominance value in the group, meaning that the ability to displace others becomes more advantageous. An increase in predation means an increase in predation mainly on individuals at the fringe of the group. The space in the centre becomes more valuable and individuals with the ability to obtain it have a higher probability to reproduce and propagate their dominance.

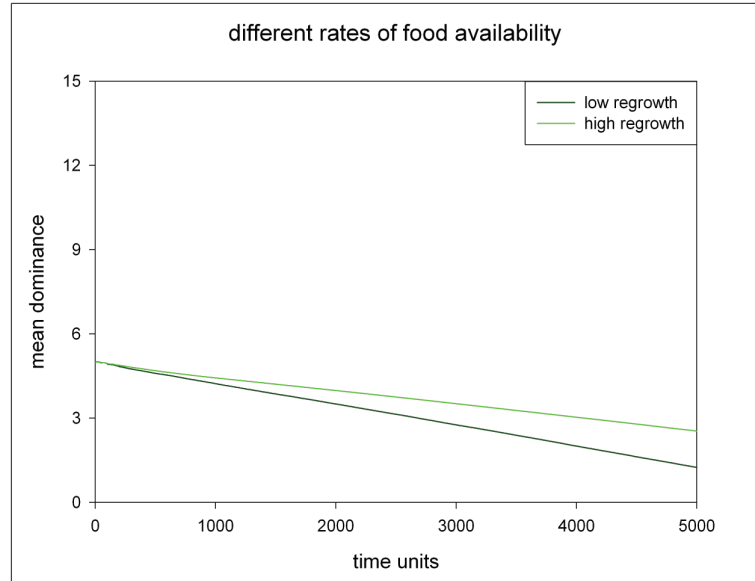


Figure 6.3: Development of average dominance for conditions with high or low rates of food availability

The first set of experiments was run in order to test the basic dynamics of the model. In the experimental condition the fleeing distance of the subordinate individuals was twice as far as the chasing distance of the dominant agents. In the control condition the chasing distance and the fleeing distance were the same. The configuration of the environmental variables in the conditions with and without displacement was chosen to enable a stable running of the model and to simulate in the control condition an environment in which the average dominance value in the group is stable in order to test the effects of the experimental variables. This configuration was based on the results of various test runs.

Despite the fact that the results of the test runs showed a stable average dominance value, the result of the 50 actual runs shows a slight decrease of the average dominance value. This illustrates the difficulty of exactly adjusting an agent based model with different interacting variables. Especially with agent based models it is necessary to find a variable setting which enables a stable running of the initial model. In order to do so many preliminary test runs are necessary. After each test run new adjustments have to be made and then the model needs to be rerun to test whether the adjustments lead to the needed stability. One of the problems is that some instabilities become visible only after many test runs, making in turn a new set of adjustments and test runs necessary. Additionally this problem increases with the increase of the number of integrated variables.



This makes the actual test running and adjusting process of a agent based model very time consuming.

Nevertheless the control condition still serves to illustrate the relative selective pressure due to the change of the fleeing distance as independent variable. Assuming that there is sufficient food in the environment, the ability to displace another individual and maintain a central position in the group in an environment with predation leads to an increase of dominance in the group. This shows that the basic dynamics of the model work. If dominant individuals are able to displace subordinate individuals they aggregate in the centre of the group and due to the higher predation pressure on the fringes the average dominance in the group increases.

The second set of experiments tests the effects of predation pressure and food availability in interaction with displacement behaviour on the development of the average dominance value in the population. In the absence of predation the dominance decreases. It decreases faster if less food is available, meaning that being in the centre of the group also has a cost. Without predation individuals can roam freely on the fringes of the group and find more food than in the centre, resulting in a higher reproduction rate of individuals with a relatively small dominance value. This in turn results eventually in a decrease of the average dominance value in the group. If there is less food available in the environment this effect is emphasised. One interpretation of this result could be that in an environment without predation and restricted resources it is more advantageous to be on the fringe of the group where the access to food is relatively high. The less food is available in the centre of a group, the more it is advantageous to be at a position outside of the centre. This could be called “fringe effect”, because if dominance is based on displacement ability, subordinate individuals are always driven to the fringe of the group.

These results could be seen as an additional argument for the position that predation was the initial reason for the selection towards dominance behaviour. Since the tested experimental conditions in the modelling environments (without food restriction or without predation) are ideal conditions which rarely exist as such in the wild, the results have to be seen as hypothetical maximum effects of a continuum. In the wild there is of course always a trade-off between being in the centre of the group and having restricted food resources, and being on the

fringe of the group and being exposed to more predation. The necessity for group living individuals to find the optimal position in this trade-off situation could in the long run facilitate the evolution of the more cognitively demanding social strategies we can observe in social groups in different animals today.

## 6.6 Conclusion

The data of many empirical observations in primate species shows that dominance usually goes together with a central position in the group (Collins, 1984). From these empirical findings and from the results of the model it is possible to conclude that the initial reason for the evolution of social structures could have been the adaptiveness of displacement behaviour due to predation pressure. The ability to displace other group members might have been based on individual differences in physical strength caused by genetic variation and can be used as a parsimonious definition of dominance. The adaptiveness of displacement behaviour results over generations in an increase of traits associated with dominance in a species.

As mentioned before it could be hypothesised that the limits of an increase in size and therefore in dominance, the amount of energy an organism needs to consume forces individuals to “invent” more efficient ways to obtain ever higher dominance positions than just increase in size. More efficient forms of obtaining higher dominance could be social strategies like cooperation with other individuals or formations of coalitions.

It is possible that social dominance is an evolved characteristic of gregarious lifestyle. The emergence of dominance was possibly the starting point for more complex interaction patterns and social structures. It is likely that with the emergence of social dominance agglomerations of individuals changed into social groups.

From the results of this model it is not possible to deduce what kind of social structure might or might not be adaptive in certain environmental situations, because the DIM does not presume any specific type of social structure. Therefore in a next step the influence of environmental pressures on the adaptiveness of already existing social structures was tested. In order to do so the environmental

factors influencing and spatial characteristics describing egalitarian or despotic social groups brought forward by van Schaik (1989) on one hand and Thierry (1990) on the other were implemented, tested and compared to the background information from the socio-ecological theory.

# Chapter 7

## Testing the coherence of the socio-ecological theory

### 7.1 Introduction

The *Macaque Social Interaction* model (hereafter the MSI) is an extension of the model discussed in the previous chapter. Its goal is to test the coherence of the socio-ecological theory (van Schaik, 1996). The MSI model is divided into two parts. In the first part the effects of predation pressure and food availability on the development of the population size of two species with different social structures in the same environment are tested. In a second part food distribution patterns — monopolisable or not — are added as third independent variable to the model.

### 7.2 Macaque Social Interaction Model – Predation and Food availability (MSI-step1)

The socio-ecological theory proposes that environmental factors are the main reason for the differences in the social structure of different primate species (see section 3.4). It names three main environmental factors forcing primates

to change their inter-individual interaction patterns (van Schaik, 1989). These factors are predation, food-availability and food distribution. The different social structures are defined as despotic or egalitarian (see chapter 3).

As mentioned in section 3.5 the differences between the species are based on two different factors. The first factor is the spatial distribution of the individuals in these different groups. According to the SET despotic agents are more despotic because they are forced closer together by predation (van Schaik, 1989). They have therefore a closer spatial distribution compared to egalitarian agents. This is in accordance to Hamilton's theory about group formation (Hamilton, 1971). This differs from Thierry's observations. He states that despotic species have a wider spatial structure due to the avoidance of potentially costly aggressive interactions (Thierry, 1986b, 1990). The other difference between the two social groups is how tolerant the agents are in their social interactions. This tolerance manifests itself in the type and frequency of interaction between members of a species (section 3.3, page 34).

In the socio-ecological theory it is assumed that high predation pressure leads to more despotic social structures, because it forces the individuals closer together and therefore the inter-individual interactions become more intense (van Schaik, 1989). It also makes predictions about the influence of food distribution on social structure. If food resources are distributed in large clumps they are monopolisable on a group level and according to the theory this promotes egalitarian behaviour. On the other hand if the food resources are distributed in small clumps and are monopolisable on an individual level despotic behaviour is promoted. In the SET four different types of social organisations are defined, from which two are relevant in genus *macaca* (Table 3.3). In this model the environmental conditions and social structures of *Type B* and *Type D* are simulated. These two types were chosen, because they represent the most common combination of environmental conditions primates and especially macaques can be found in.

## 7.2.1 Methods

### Agents

The MSI-step1 is based on the dominance inheritance model from the previous chapter. In order to test the predictions of the socio-ecological theory, some extensions were implemented into this model. In a first step two different types of agents were integrated. One represents a species with a more egalitarian social structure, the other represents a more despotic social structure. Both types of agents were integrated into the same environment. The two agent “species” were ignorant of each other.

The difference between the two types of agents in the model are based on the two factors mentioned above. One difference is the spatial distribution, the other is the “tolerance” of the agents. As in the dominance inheritance model each agent has a repertoire of different behaviours. Agents can move around in a random fashion, search for food, feed or engage in interactions with other agents. They also reproduce and die. Each agent has a *maximum group distance*, a *comfort distance* and a *personal space*. The personal space represents its immediate proximity, the comfort distance a close-by area around the agent and the maximum group distance, represents the maximum distance an agent will wander away from all other agents of its group. These parameters correspond to the parameters used in the dominance inheritance model (section 6.3.1).

According to the socio-ecological theory egalitarian agents have wider spatial distribution than the despotic agents. This is implemented into the model in such a way that the *maximum group distance* of egalitarian agents is bigger than the *maximum group distance* of despotic agents resulting in a less cohesive group structure for the egalitarian agents (Reynolds, 1987). The tolerance level of the agents in the model is represented by the size of their *personal space*. A smaller personal space represents a higher tolerance. For despotic agents the *personal space* is bigger than the *personal space* of egalitarian agents accounting for their less tolerant behaviour.

As in the dominance inheritance model, each agent has a dominance value, defining its position in the hierarchy of the group. This dominance value is randomly

assigned to the agents at the beginning of the simulation. The higher the dominance value, the higher the position in the hierarchy of the group. If an agent reproduces, its offspring inherits its dominance value with a some small variation.

Every time step each agent checks the position of the agents surrounding it. If an agent detects other agents of its group within its comfort distance it roams around freely in a random fashion or pursues food. If it, by doing so, moves too far away from the centre of its group (too far is defined by the maximum group distance) it will start to move towards the group centre until it detects another agent in its comfort distance. Like in the dominance inheritance model the centre of the group of an agent is represented by the sum of the x-coordinates of all other agents in its vision radius divided by their number and the sum of the y-coordinates of all other agents in its vision radius divided by their number. The vision radius of an agent represents the distance in which it considers other agents to be members of its group and is a predefined variable. This way of calculating the centre of a group follows the idea of Hamilton (1971). As discussed in section 2.3 the safest place for an individual is to be as close as possible to a conspecific.

If an agent detects other agents of its group within its personal space, a social interaction between these agents is initiated. This social interaction is similar to the dominance interaction described in section 6.3.1. Like in the *Dominance Inheritance Model* the dominance values of the opponents stay the same after an interaction so we refer to this as a displacement, not a fight. The fleeing distance in this model is always twice as far as the chasing distance because as the results of the *Dominance Inheritance Model* show, predation has only an effect on the average dominance value in a group, if the outcome of a fight has a spatial consequence.

## Environment

The simulation environment has the size of 241 x 241 patches. Like in the *Dominance Inheritance Model* a patch is a squared raster element representing a spatial unit. The setup of the patches is essentially the same as in the *Dominance Inheritance Model*. Initially each patch has a food-value assigned to it and is therefore classified as food patch. If an agent moves over a food patch it adds the food-value of the patch to its own energy value. After this the food-patch is set to

empty. It stays empty for as long as the regrowth-time is set. This is how feeding is defined in the model.

Similar to the dominance inheritance model each agent has an energy value assigned to it in the beginning of the simulation or after its birth. This energy value is reduced every time the agent moves. The agents feed whenever they move over a food patch and below a certain energy level feeding becomes their highest priority (affecting their navigation). Once the value drops under a certain threshold, the agent starts to search for food. After the search for food is initiated the agent “looks” for the closest patch with a food-value in a certain predefined radius. It then turns toward this patch and moves over it. By doing so the agent adds the food-value of the patch to its own energy-value. It repeats this sequence until its energy-value is above the threshold by which the search for food behaviour is triggered. If however the closest patch with a food-value is further away than an agent has energy left to move to it, the agent dies.

Like in the dominance inheritance model the food availability depends on the *regrowth rate*. The *regrowth rate* defines the percentage of the empty patches which changed into food patches after a predefined time interval. The *regrowth rate* is one of the two independent variables in the MSI-step1 and can either be relatively high or low.

Each agent has an energy value as described above. In order to reproduce, the agent has to reach a certain energy threshold. The agent will then spawn one offspring which will inherit the dominance value of its parent. After spawning the energy value of the parent is reduced by the reproduction cost. Reproduction cost is a variable which is set in the beginning of the simulation. The offspring will start to move around randomly right after its spawning.

In the model predation pressure is, like in the *Dominance Inheritance Model*, implemented as statistical predation. A percentage of the population is killed after a predefined time period. The distance of each agent to the closest neighbour of its group is written into a list. The list is then sorted by size, starting from the highest. During the predation procedure the agents on top of this list are killed, because they are furthest away from any other agent. How many agents from the list are killed depends on the percentage given in the predation-pressure parameter. Predation pressure is the second independent variable in this model



and can either be relatively high or relatively low.

Variable	Setting
clustering	on or of
predation rate	2.7 or 8.7
regrowth-rate	20 or 60
food density	80 or 100
reproduction costs	27 or 15
population size	20
hunting time	10
energy costs	4
foodvalue	6
EgalPerspace	3
EgalNearView	15
EgalMaxView	40
DespPerspace	6
DespNearView	15
DespMaxView	20
vision-radius	40

Table 7.1: Initial parameter settings for the MSI-step1 and MSI-step2 models

## Experimental Setup

In order to test the independent effects of high and low predation pressure and high and low food availability on the development of the average population size a first set of experiments with four different experimental conditions was run (see Table 7.2).

In order to test the interaction effects of different rates of predation pressure and food availability on the successfulness of the two agent groups a second set of experiments was run. This second set of experiments contained also of four different experimental conditions (see Table 7.3).

Condition	Setup	Label
1	low predation / average food availability	LP
2	high predation / average food availability	HP
3	low food availability / average predation	LR
4	high food availability / average predation	HR

Table 7.2: Experimental setup - Independent effects

Additionally to the population size, which was used as a measure for the successfulness of the groups, the number of agents killed by predation, the number of agents born and the number of agents starved was measured for each group to understand the dynamics of the model better.

The exact values used in the experimental conditions for predation pressure and food availability (high, average and low) and the values shown in table 7.1 were chosen in a comparable process to the one described in section 6.5. After the main implementation process numerous test runs were conducted with the model. The aim of these test runs was to find a configuration which allowed the stable running of the model over long periods of time without having the agent populations die out. This is necessary to get meaningful results for the dependent variables. This stable configuration represents the average setup of the model. According to the assumptions of the hypotheses the settings for the independent variables (high or low) were found in another set of test runs. The final experimental configuration was chosen based on the outcome of these test runs. In a condition with high predation pressure and low food availability for example, which represents the harshest environment for the agents in the model, a configuration had to be chosen which enabled the agents to survive for the entire length of an experimental run in at least most of the cases, because having them die out right after the experimental run started would produce no usable results. Using this “minimum” configuration the other values were set according to the questions to be answered.

Condition	Setup	Label
1	low predation / high food availability	LP/HR
2	high predation / low food availability	HP/LR
3	low predation / low food availability	LP/LR
4	high predation / high food availability	HP/HR

Table 7.3: Experimental setup - Interaction effects

## 7.2.2 Results

In order to examine the interaction effects of predation pressure and food availability, the two variables were at first tested independently and then together. As statistical method to test the significance of the differences between the conditions the t-test was used.

### Population size

The results for the average population size in the condition with low predation pressure show that the egalitarian population is bigger than the despotic population. The difference is significant (LP [N = 100,  $t = 26.54$ ,  $p < .001$ ]). The opposite is true for the condition with high predation pressure. Here the number of despotic agents is bigger. This difference is also significant (HP [N = 100,  $t = 7.48$ ,  $p < .001$ ])). Both conditions were run with a stable average food availability (Figure 7.1(a)).

The results for the average populations size in the condition with low food availability show that the number of agents in the egalitarian group is significantly bigger than in the despotic group (LR [N = 100,  $t = 17.27$ ,  $p < .001$ ]). The results for the condition with high food availability show that the number of agents in the despotic group is significantly higher than in the egalitarian group (HR [N = 100,  $t = 21.97$ ,  $p < .001$ ])). Both conditions were run with a stable average

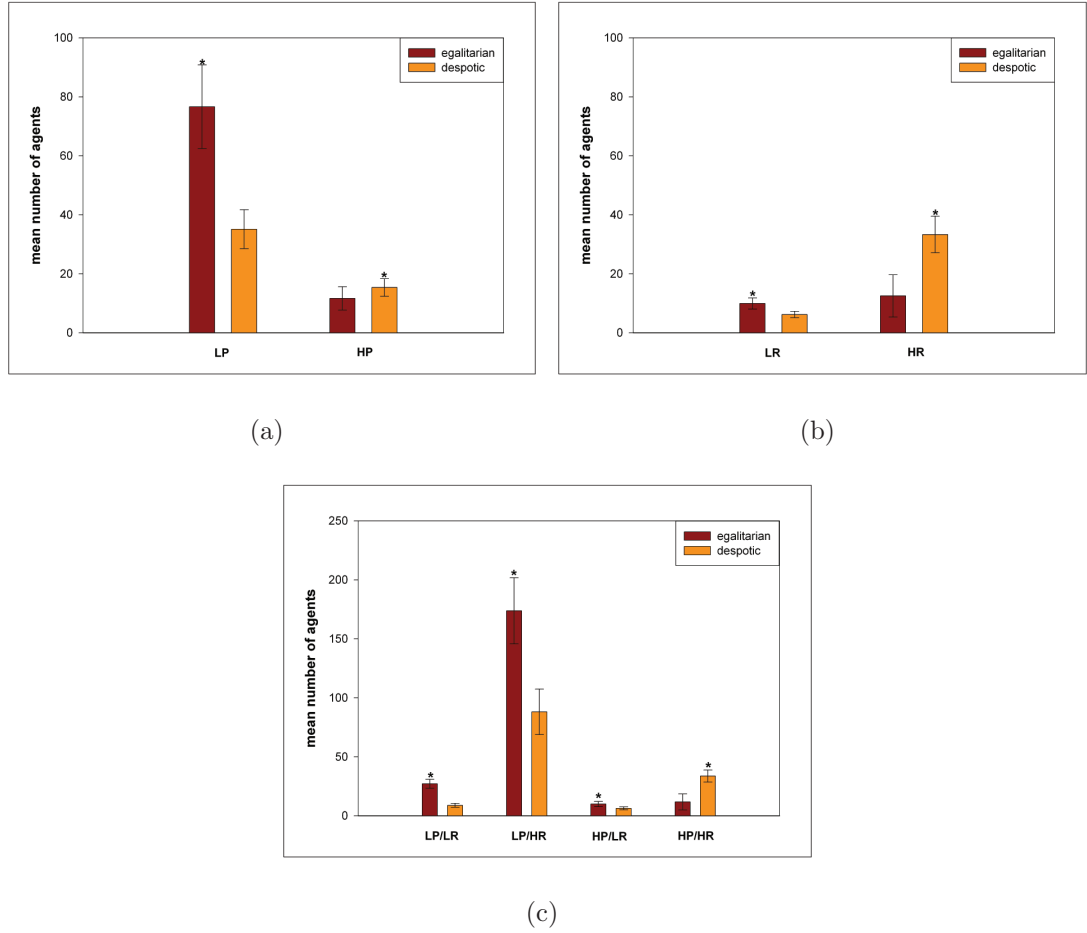


Figure 7.1: Average population size for conditions with high or low predation pressure and an average stable regrowth rate (a), high or low food availability and an average stable predation rate (b) and for the interaction effect of predation pressure and food availability (c)

predation pressure (Figure 7.1(b)).

The results for the interaction effect of predation pressure and food availability on the average population size show that the egalitarian population is significantly bigger in three of the four experimental conditions (LP/LR [ $N = 100$ ,  $t = 43.94$ ,  $p < .001$ ], LP/HR [ $N = 100$ ,  $t = 25.19$ ,  $p < .001$ ]) and HP/LR [ $N = 100$ ,  $t = 14.49$ ,  $p < .001$ ]). The despotic population is only bigger in the condition with high predation pressure and high food availability (HP/HR [ $N = 100$ ,  $t = 25.8$ ,  $p < .001$ ])(Figure 7.1(c)).

## Number of offspring

These results show that regardless of different rates of predation pressure the number of offspring is significantly higher in the egalitarian population (LP [ $N = 100$ ,  $t = 31.33$ ,  $p < .001$ ], HP [ $N = 100$ ,  $t = 9.27$ ,  $p < .001$ ]). Both conditions were run with a stable average food availability (Figure 7.2(a)).

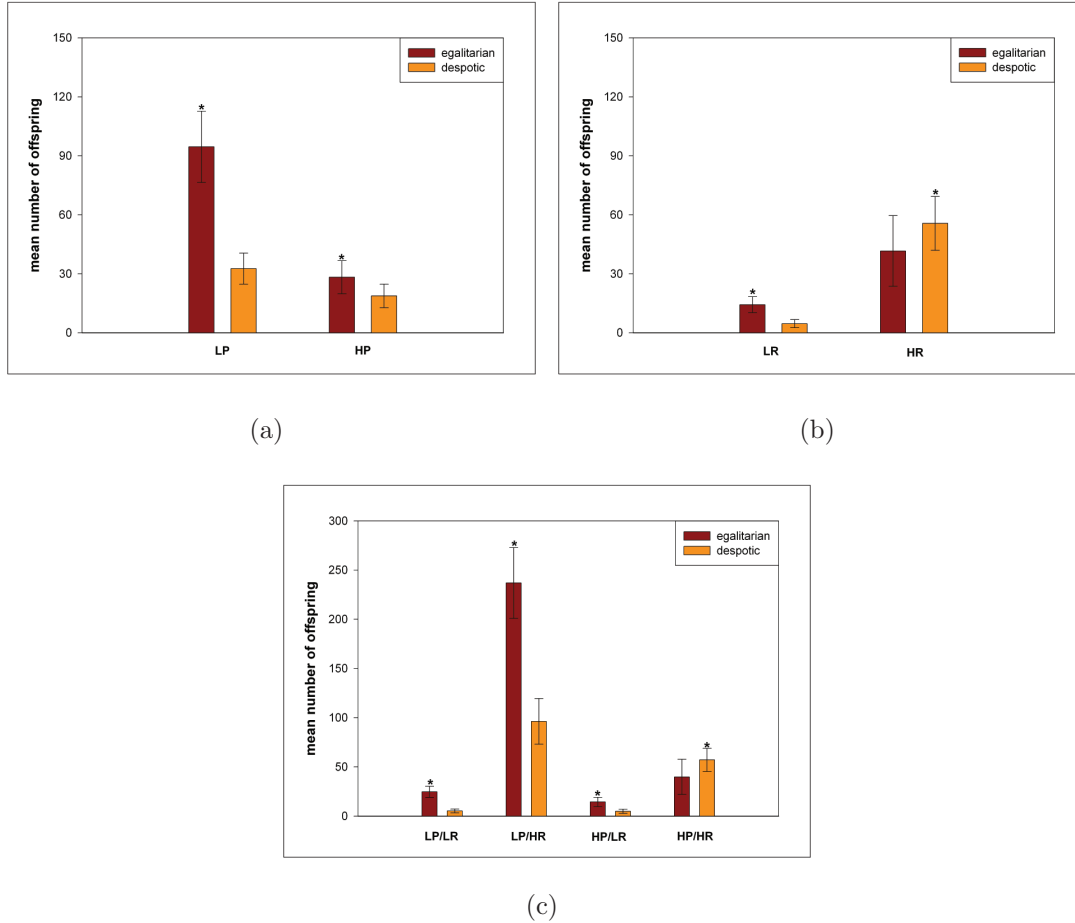


Figure 7.2: Average number of offspring for high and low predation rates and a stable average food availability(a), high and low food availability and a stable average predation pressure(b) and for the interaction between predation and regrowth rates (c)

However different rates of food availability affected the different populations differently. For the condition low food availability show the number of offspring in the egalitarian population is significantly higher than in the despotic population (LR [ $N = 100$ ,  $t = 21.4$ ,  $p < .001$ ]). For the condition with high food availability the number of offspring in the despotic population is significantly higher than in the egalitarian population (HR [ $N = 100$ ,  $t = 6.22$ ,  $p < .001$ ]). Both conditions

were run with a stable average predation pressure (Figure 7.2(b)).

The results for the interaction effect of predation pressure and food availability on the number of offspring show that the egalitarian agents produce significantly more offspring in three of the four experimental conditions (LP/LR [N = 100, t = 32.63, p < .001], LP/HR [N = 100, t = 32.83, p < .001]) and HP/LR [N = 100, t = 18.89, p < .001]). The despotic agents produced significantly more offspring only in the condition with high predation pressure and high regrowth-rate (HP/HR [N = 100, t = 8.09, p < .001])(Figure 7.2(c)).

### **Number of agents starved to death**

The results for the number of starved agents show that regardless of different rates of predation pressure (LP [N = 100, t = 6.92, p < .001], HP [N = 100, t = 13.3, p < .001])(Figure 7.3(a)) and also regardless of the different rates of food availability significantly more agents starved to death in the despotic population (LR [N = 100, t = 24.44, p < .001], HR [N = 100, t = 6.16, p < .001])(Figure 7.3(b)).

The results for the interaction effect of predation pressure and food availability show that in three of the four experimental conditions significantly more despotic agents died of starvation (LP/LR [N = 100, t = 16.67, p < .001], HP/LR [N = 100, t = 30.02, p < .001], HP/HR [N = 100, t = 5.47, p < .001]). Only the results for the condition with low predation pressure and high food availability shows no significant difference (LP/HR [N = 100, t = 1.47, p = .14])(Figure 7.3(c)).

### **Number of agents killed by predation**

The last set of results analysed in the MSI-step1 is the number of agent killed by predation. The results for the number of agents killed by predation show that regardless of the different rates of predation pressure (LP [N = 100, t = 37.42, p < .001], HP [N = 100, t = 25.09, p < .001])(Figure 7.4(a)) and also regardless of different rates of food availability (LR [N = 100, t = 34.09, p < .001], HR [N = 100, t = 5.28, p < .001])(Figure 7.4(b)) significantly more agents get eaten in the egalitarian group. The conditions with different rates of predation were run

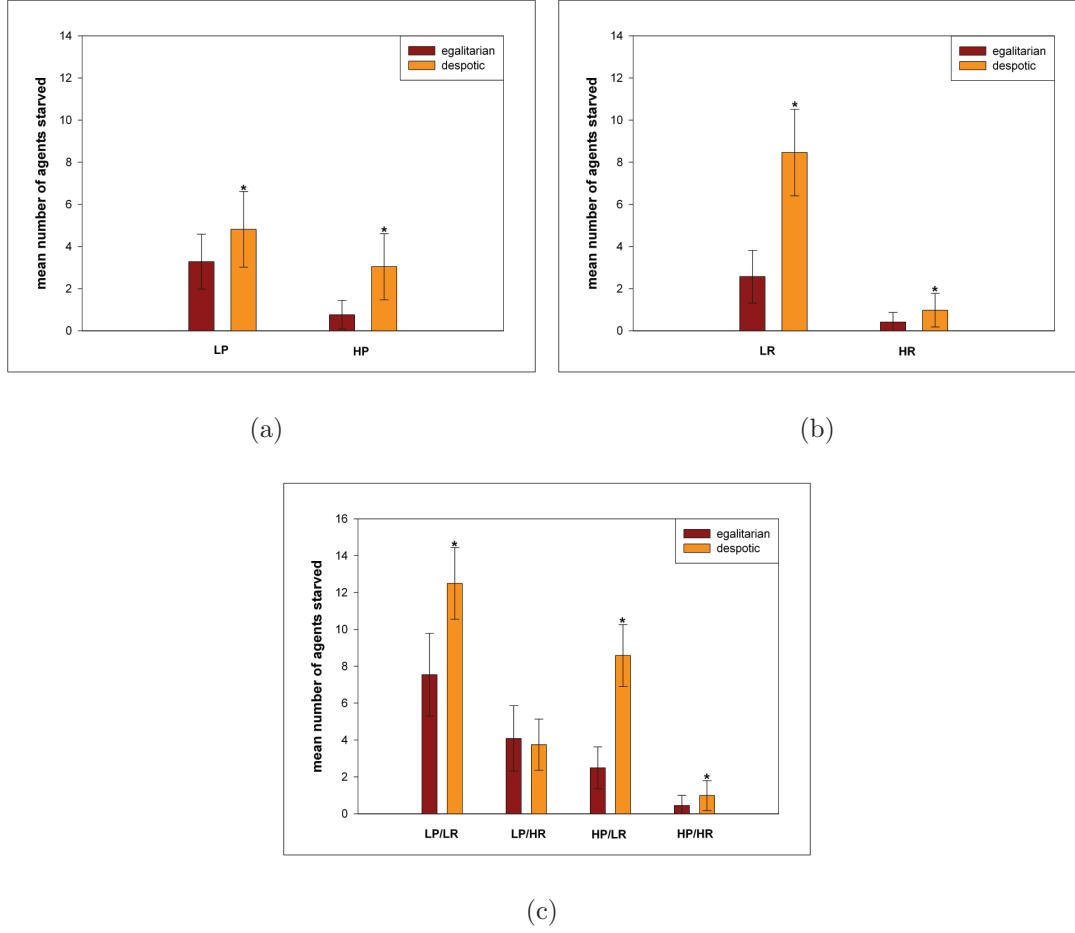


Figure 7.3: Average number of starved agents for high and low predation rates and a stable average food availability (a), high and low food availability and a stable average rate of predation (b) and for the interaction between predation and regrowth rates (c)

with a stable average food availability and the conditions with different rates of food availability were again run with a stable average predation pressure.

The results for the interaction effect of predation pressure and food availability show that significantly more agents are killed by predation in all four experimental conditions in the egalitarian population (LP/LR [ $N = 100$ ,  $t = 31.06$ ,  $p < .001$ ], LP/HR [ $N = 100$ ,  $t = 49.91$ ,  $p < .001$ ], HP/LR [ $N = 100$ ,  $t = 18.89$ ,  $p < .001$ ], HP/HR [ $N = 100$ ,  $t = 3.8$ ,  $p < .001$ ])(Figure 7.4(c)).

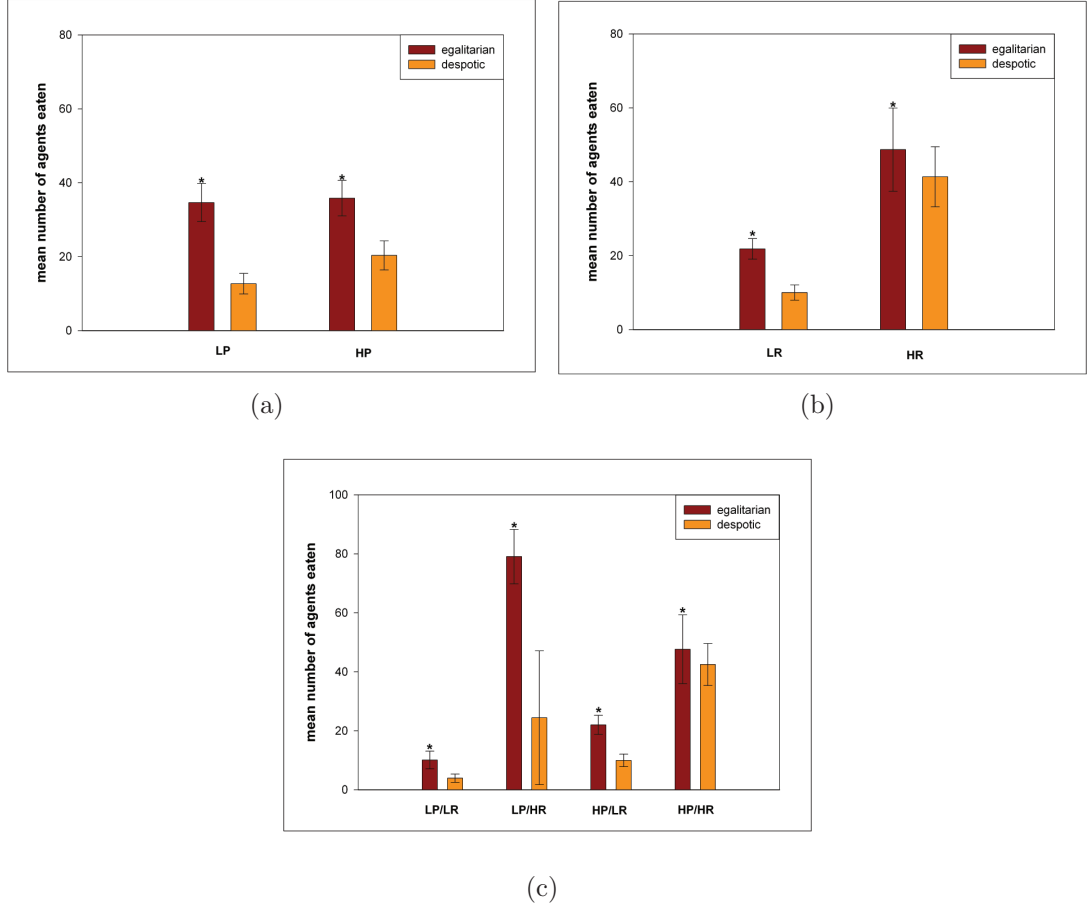


Figure 7.4: Average number of agents killed by predation for high and low predation rates and a stable average food availability (a), high and low regrowth rates and a stable average predation pressure (b) and for the interaction between predation and regrowth rates (c)

### 7.2.3 Discussion — MSI-step1

As mentioned in section 7.2.1 the population size is in the model the measure for the successfulness of the groups and the results for the number of offspring, of starved and killed agents were measured in order to be able to understand and interpret the dynamics of the model better. Therefore the focus of the discussion will be on the population size results.

The results for the population size can be split into two categories. The first category deals with the independent effects of predation pressure and food availability and the second category with the interaction effects of different rate of predation pressure and food availability on the two agent groups.



The results for the independent effects show that the egalitarian population was more successful in terms of size than the despotic population in conditions with low predation pressure and in conditions with low food availability. The despotic population on the other hand was more successful in conditions with high predation pressure and with high food availability. Looking at the outcome for the number of agents killed by predation, the number of starved agents and the number of offspring the reason for these results becomes clear. In all conditions more egalitarian agents were killed by predation due to their wider spatial structure. On the other hand in all conditions more despotic agents died of starvation due to their dense spatial structure. The results for the number of offspring show a slightly different structure. In three of the four conditions the egalitarian agents produced more offspring. Only in the condition with high food availability was the number of offspring generated by the despotic agents higher.

The population size of the egalitarian agents was therefore bigger than the population size of the despotic agents in the condition with low predation, because the number of egalitarian agents killed by predation and starved was in relation to the offspring they produced relatively smaller than this was the case for the despotic agents. The opposite is true for the condition with high predation. Although the egalitarian agents produced more offspring than the despotic agents, in relation to this number the number of agents killed due to predation and starvation was relatively smaller in the despotic population than in the egalitarian population. The results for the different rates of food availability in the environment can be explained with the fact that in the model low food availability has a strong negative effect on the despotic population and that the opposite is true for high rates of food availability. In the low food availability condition in relation to the produced offspring the number of starved agents was relatively high in comparison to the condition with high food availability. Also with high food availability the despotic agents produced more offspring than the egalitarian agents.

The fact that in the conditions with high food availability and average food availability in combination with high predation only one egalitarian agent died of starvation illustrates that due their wider spatial structure the egalitarian agents are only very marginal effected by possible food availability restrictions in the model.

The results above have to be seen as the independent effects of predation pressure and food availability in the model because as described in section 7.2.1 the average rates for predation pressure and food availability represent the average setup of the model, meaning the model runs under these conditions stable (with stable populations) over the entire length of an experimental run. In the first set of experiments only one of the two test variables was manipulated (high or low). The other test variable was kept with the setup from the stable model configuration.

The results for the interaction effects of food availability and predation show that the despotic population was only more successful in terms of size compared to the egalitarian population in the condition with high predation pressure and high food availability. In the other three conditions (see Table 7.3) the population of the more egalitarian agents was bigger. Like in the results for the independent effects, the results for the number of offspring, the number of agents killed by predation and the number of agents starved explain these results. In all four conditions more egalitarian agents were killed by predation. But in contrast to the results of the independent effects there was no difference between the number of despotic and egalitarian agents starved to death in the condition with low predation pressure and high food availability. This condition represents the optimal environmental conditions for both species. This is the reason why both species perform much better in this variable configuration compared to the three other conditions. Nevertheless due to the structure of the reproduction mechanism, in order to reproduce an agent needs to find more food quickly, the egalitarian agents have an advantage due to their wider spatial structure compared to the despotic agents. The results for the number of offspring show that despotic agents produced more offspring only in the condition with high predation pressure and high food availability. These results of the interaction of predation pressure and food availability confirm the results from the independent effects that predation pressure in the model has a stronger negative effect on the egalitarian agents and restricted food availability on the despotic agents. They also confirm that in conditions with sufficient food and low predation pressure the egalitarian agents can reproduce faster due to their wider spatial structure.

A further analysis of the meaning of these results and an interpretation as well as a critical discussion of both the MSI-step1 and the MSI-step2 models will be carried out in section 7.4.

## 7.3 Macaque Social Interaction Model – Food distribution (MSI-step2)

The MSI-step2 represents an extension to the MSI-step1. Additionally to the two independent variables of the previous model, the aim of this extension is to test the effects of spatial patterns of food distribution as a third independent variable. The implementation of food distribution patterns is based on the hypothesis of the *SET* that this also has a major influence on the form of social structure in primate groups.

### 7.3.1 Clumped food as additional factor in the MSI-step1

In MSI-step1 every patch was a potential food patch. This has to be changed in order to model an environment with clumped food resources. In order to do so, the setup of the environment had to be changed in such a way that it could contain food patches and empty patches which could not become food patches during a simulation. Two new variables called *food density* and *food distribution* were implemented into the MSI-step2 to achieve this.

*Food density* determines the percentage of patches in the environment which are potential food patches. A *food density* of 50% for example would represent an environment in which only half of the patches could become food-patches. Food-patches are defined in the same way they are defined in the MSI-step1 model (section 7.2.1).

The *food distribution* variable can have two instances, which also represent the two additional conditions in the MSI-step2. They are called *non-clustered* and *clustered* food distribution. As described above, the amount of food is determined by *food density*. In the *non-clustered* condition the food patches and the empty patches are distributed randomly in the environment in the beginning of a simulation resulting in spread out, randomly distributed food resources (see Figure 7.5(a)).

In the *clustered* condition the food is in a first step randomly distributed in the

environment, but in a second step each food patch changes its status according to the states of the majority of the patches adjacent to it. This results in an environment with clumps of food-patches and clumps of empty patches (see Figure 7.5(b)). The size of the patches depends on the food available in the environment. The less food in the environment the smaller the patches.

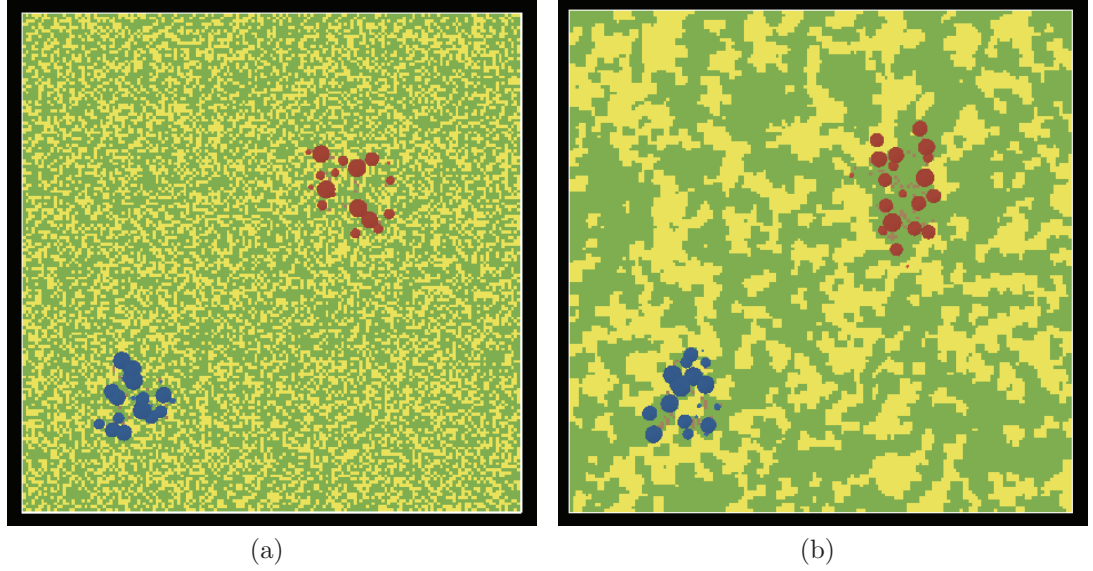


Figure 7.5: Images of the non-clustered (a) and clustered (b) food distribution conditions. The green patches represent food patches, the yellow patches empty patches and the blue and red dots represent groups of agents with different spatial distributions.

The feeding procedure worked the same way as in the MSI-step1 (section 7.2.1). The only difference is the existence of empty patches. They stay empty during the entire simulation. If agents move over them, empty patches don't change their status. An agent can extract energy only from "filled" food patches.

In order to compensate for the effects of less overall food in the environment and prevent an "extinction" of one or both of the different populations in certain conditions, it was necessary to adjust the value of the energy an agent needed to reproduce according to the rate of food reduction. Therefore the *reproduction cost* (see section 6.3.1) was reduced.

For the MSI-step2 the experimental structure of the MSI-step1 was repeated for both the *non-clustered* and *clustered* food resource setting. First both the *non-clustered* and *clustered* settings were run with different rates of predation pressure and a stable average food availability. Then they were run with different food

availability rates and a stable average predation pressure. In a third step both conditions were run with different rates of food availability and different rates of predation pressure.

The *non-clustered* condition represents essentially the environmental condition of MSI-step1 only with less food and empty patches in the environment. The results of the non-clustered condition were used to compare them to the results of the clustered condition and also to compare them to the main results of MSI-step1 in order to test the effect of the existence of empty patches in the environment.

The simulation was run 100 times for each condition for a predefined number of time steps and for each of the 16 different conditions. The initial parameter settings for the MSI-step2 model can be found in table 7.1. The results were analysed in two different ways. First the population size of the despotic and the egalitarian group in each of the conditions explained above was compared with each other. After that the population sizes of the despotic group in the non-clustered and in the clustered condition were compared with each other. The same was done with the results of the egalitarian group.

### 7.3.2 Results

Like in the MSI-Phase1 four dependent variables were measured (average population size, number of offspring produced, number of agents starved and number of agents killed by predation) for both the despotic and the egalitarian population. And also like before the average population sizes represent the main result of the experiments.

#### Results for the *non-clustered* condition

In a first step the non-clustered condition was tested. It essentially represents the environmental condition of the MSI-step1, only with less food resources. Since the results for the three secondary dependent variables (number of offspring, number of starved and of predated agents) largely match the results of the MSI-step1, only the main result the population size is presented at this point. The results

for the secondary independent variables are in the appendix (12.1.1).

**Population size:** With a stable average food availability the size of the egalitarian population was bigger than the size of the despotic population in the condition with low predation pressure (LP [ $N = 100$ ,  $t = 14.12$ ,  $p < .001$ ]). In the condition with high predation pressure the despotic population was bigger (HP [ $N = 100$ ,  $t = 7.46$ ,  $p < .001$ ])(Figure 7.6(a)). Both differences were significant.

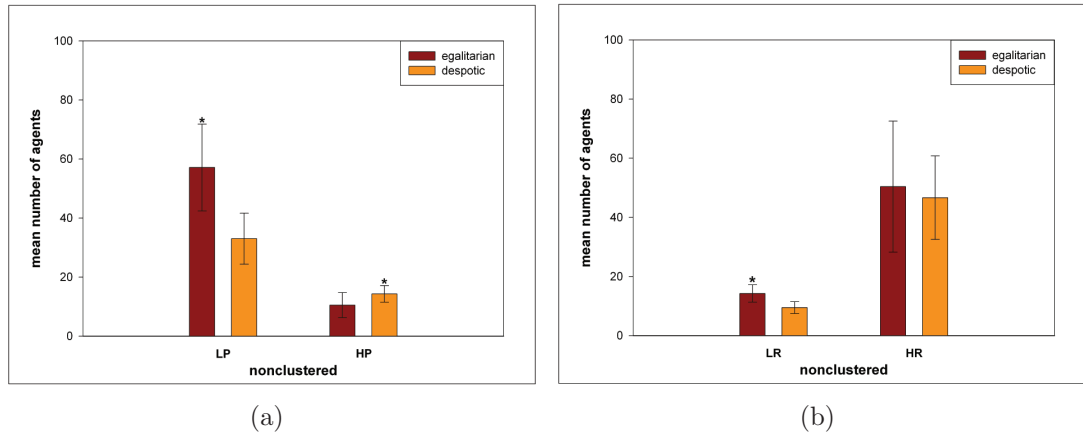


Figure 7.6: Average population sizes for high and low predation pressure (a) and high and low food availability (b) in the *non-clustered* condition

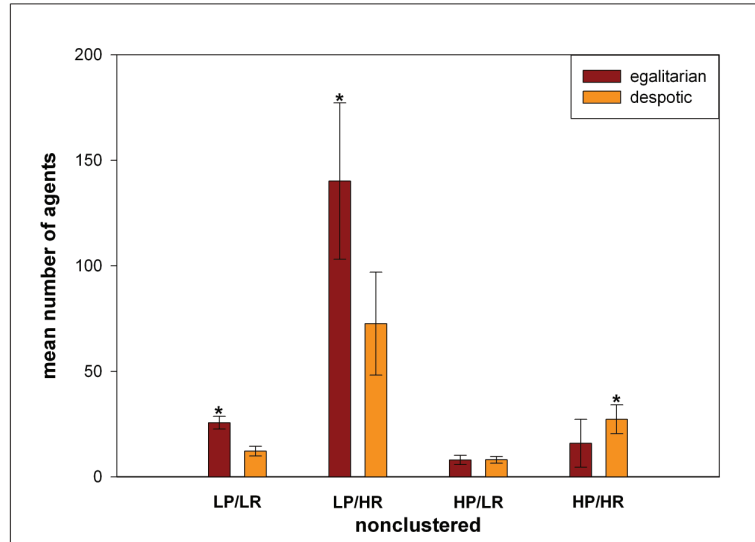


Figure 7.7: Average population sizes for the interaction between the different rates of predation and food availability in the *non-clustered* condition

With stable average predation pressure the egalitarian population was significant-

antly bigger in the condition with low food availability (LR [N = 100, t = 13.5, p < .001]). In the condition with high food availability and stable average predation there was no significant difference between the two populations (HR [N = 100, t = 1.42, p = .15])(Figure 7.6(b)).

The results for the interaction effects of predation rate and food availability show that the egalitarian population was significantly bigger in two of the four different conditions (LP/LR [N = 100, t = 35.46, p < .001], LP/HR [N = 100, t = 15.22, p < .001]). The despotic population was significantly bigger in the condition with high predation pressure and high food availability (HP/HR [N = 100, t = 8.63, p < .001]). There was no significant difference between the populations in the condition with high predation pressure and low food availability (HP/LR [N = 100, t = 0.16, p = .87])(Figure 7.7).

### Results for the *clustered* condition

In a second step the effects of clustered food resources on the population sizes of the two agent populations in combination with different rates of predation and food availability were tested. Like in the tests for the non-clustered condition also the three secondary dependent variables number of offspring, number of agents died by starvation and number of agents killed by predation were measured. Since these results were recorded to make the interpretation of the main results for the population size easier and they largely matched the results of the three secondary results of the non-clustered condition, they can be found in the appendix (12.1.1).

**Population size:** With a stable average food availability the egalitarian population was significantly bigger in the condition with low predation pressure (LP [N = 100, t = 10.82, p < .001]). The despotic population was bigger in the condition with high predation pressure (HP [N = 100, t = 2.25, p = .03])(see Figure 7.8(a)).

With a stable predation pressure the egalitarian population was significantly bigger in the condition with low food availability (LR [N = 100, t = 10.59, p < .001]). There was no significant difference between the two populations in the condition with high food availability (HR [N = 100, t = 0.97, p = .33])(Figure 7.8(b)).

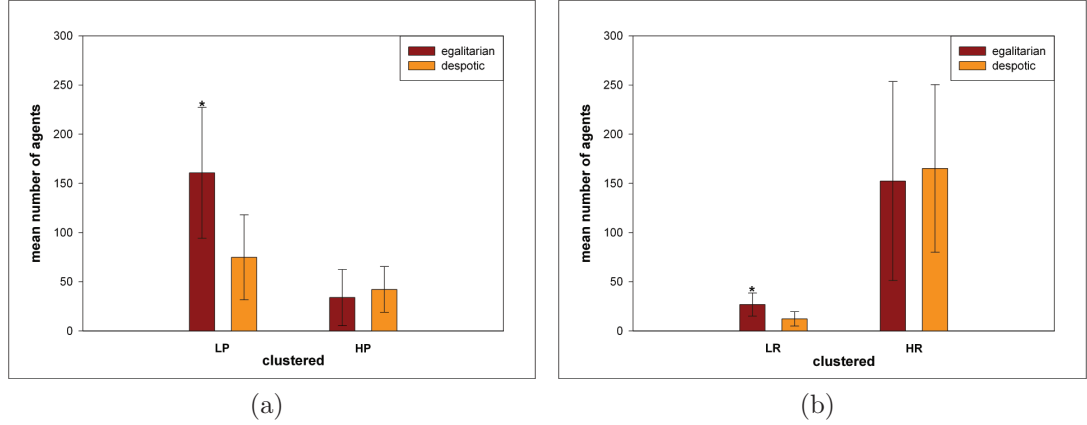


Figure 7.8: Average population sizes for high and low predation pressure (a) and high and low food availability (b) in the *clustered* condition

The egalitarian population was significantly bigger in three of the four conditions with clustered food resources (LP/LR [ $N = 100$ ,  $t = 15.5$ ,  $p < .001$ ], LP/HR [ $N = 100$ ,  $t = 3.44$ ,  $p < .001$ ], HP/LR [ $N = 100$ ,  $t = 5.22$ ,  $p < .001$ ]). The despotic population was significantly bigger in the condition with high predation pressure and high food availability (HP/HR [ $N = 100$ ,  $t = 6.63$ ,  $p < .001$ ])(Figure 7.9).

### Comparison of the results for non-clustered and for the clustered condition for each of the two agent populations

The results of the comparison of the results for number of offspring, number of starved agents and number of agents killed by predation of each the despotic and egalitarian populations in the clustered and non-clustered conditions can be found in the appendix (12.1.1).

### Population size

Despite high or low rates of predation pressure the egalitarian population was significantly bigger in the conditions with stable average food availability and clustered food sources (LP [ $N = 100$ ,  $t = 15.48$ ,  $p < .001$ ] and HP [ $N = 100$ ,  $t = 8.09$ ,  $p < .001$ ]). The same is true for the despotic population (LP [ $N = 100$ ,  $t = 9.56$ ,  $p < .001$ ] and HP [ $N = 100$ ,  $t = 11.74$ ,  $p < .001$ ])(Figure 7.10).



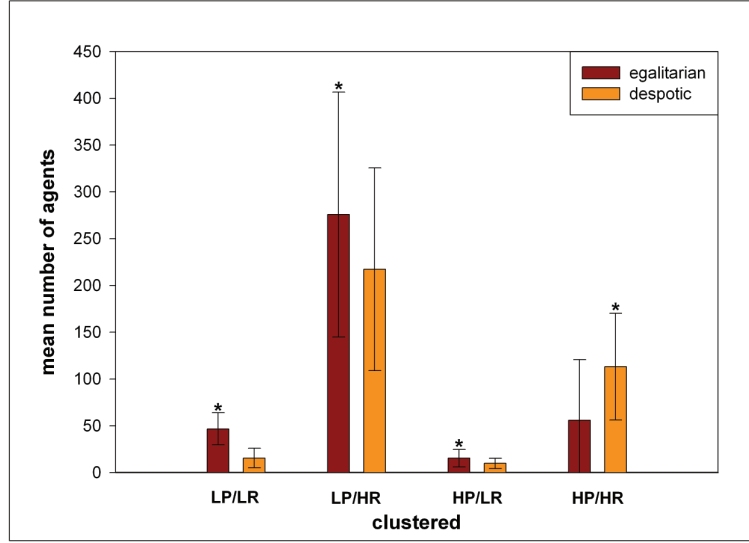


Figure 7.9: Average population sizes for the interaction between the different rates of predation and food availability in the *clustered* condition

The comparison of the population sizes in the different conditions show that the egalitarian population was significantly bigger in conditions with clustered food sources than it was in the same conditions with equally distributed food resources (LR [N = 100,  $t = 10.53$ ,  $p < .001$ ], HR [N = 100,  $t = 9.86$ ,  $p < .001$ ]). The same is true for the despotic population (LR [N = 100,  $t = 3.74$ ,  $p < .001$ ], HR [N = 100,  $t = 13.89$ ,  $p < .001$ ])(Figure 7.11).

The size of the despotic population was in the clustered setting in all four conditions with either high or low predation pressure and food availability significantly better than in the non-clustered (LP/LR [N = 100,  $t = 12.32$ ,  $p < .001$ ], LP/HR [N = 100,  $t = 10.00$ ,  $p < .001$ ], HP/LR [N = 100,  $t = 7.41$ ,  $p < .001$ ] and HP/HR [N = 100,  $t = 6.09$ ,  $p < .001$ ])(Figure 7.12). The same is true for the size of the egalitarian population (LP/LR [N = 100,  $t = 3.17$ ,  $p = .002$ ], LP/HR [N = 100,  $t = 12.73$ ,  $p < .001$ ], HP/LR [N = 100,  $t = 3.06$ ,  $p = .003$ ] and HP/HR [N = 100,  $t = 15.11$ ,  $p < .001$ ])(Figure 7.13).

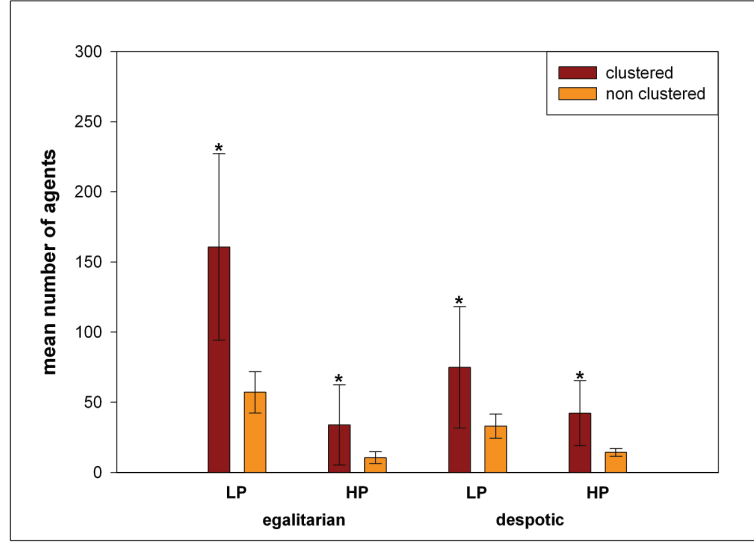


Figure 7.10: Comparison of the population sizes of the two different agent populations in the clustered vs. non-clustered condition for the different rates of predation and stable average food availability

### 7.3.3 Discussion — MSI-step2

#### Comparison of the results of the non-clustered setting

Since the non-clustered setting of the MSI-step2 was similar to the MSI-step1 model the result of the two models are also similar. This confirms that the integration of the food density variable did not change the dynamics of the model. This was important to test in order to assure the interpretability of the further results. As mentioned in section 7.3.2 the only difference between the MSI-step1 model and the non-clustered setting of the MSI-step2 model is the amount of food in the environment, because the food patches are, according to the food density, randomly distributed in the environment.

Like in the MSI-step1 model the results of this first set of experiments show that for most of the conditions the egalitarian population was bigger than the despotic population. Only in the condition with high predation pressure and in the condition with a combination of high predation pressure and high food availability the despotic agents were more successful in terms of population size than the egalitarian agents.

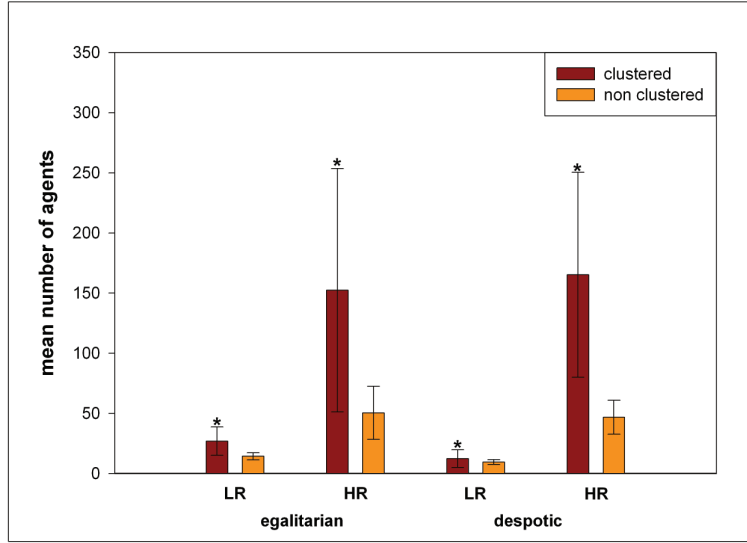


Figure 7.11: Comparison of the population sizes of the two different agent populations in the clustered vs. non-clustered condition for the different rates of food availability and stable average predation pressure

The only difference to the MSI-step1 model represent the results of the conditions with high food availability and the condition with the combination of high predation pressure and low food availability. In both conditions there were no significant differences between the two the population sizes. In the latter both the despotic and the egalitarian population were least successful, because this condition represents the harshest environmental setting for the agents in the model. The lack of significance in the result for the condition with high food availability is explainable with the lower amount of food in the environment in general. This affected the despotic population more negatively than the egalitarian population in this condition. The reason for the absence of a significant difference between the population sizes in the result for the condition with a combination of high predation and low food availability is harder to explain. In the MSI-step1 model this difference was already smaller than the differences in any other condition. In the MSI-step2 model the decreased food availability in this condition either could have effected the egalitarian population additionally in a negative way or it could have lead to even bigger inter-individual differences between the egalitarian agents, which would have made them even more vulnerable to predation.

In general it can be said that, like in the MSI-step1 model, high rates of predation had a stronger negative effect on the egalitarian population and low rates of food availability had a stronger negative effect on the despotic population. Both of

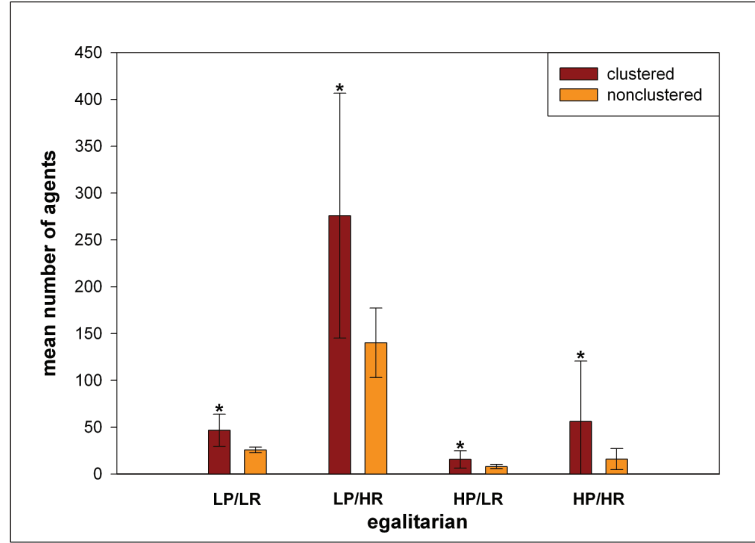


Figure 7.12: Comparison of the population size in the clustered vs. non-clustered setting for despotic agents

these effects can be explained by the characteristics of the spatial distribution of the two groups. Like in MSI-step1 model the egalitarian population always produced more offspring except in the condition with high predation and a high regrowth-rate (see appendix 12.1.1). This suggest that they reach the energy level necessary for reproduction faster than the despotics due to their wider spatial structure.

As mentioned in the beginning of this section, the experimental runs of the MSI-step2 model with the non-clustered setting can be seen as successful, because the result of these runs confirm that the implementation of the food-density variable does not affect the basic dynamics of the MSI model.

### Results for the condition with clustered food distribution

The results for the clustered setting of the MSI-step2 model show that like in the non-clustered setting the egalitarian population was in most of the conditions bigger than the despotic population and that only in the condition with a combination of high predation and high food availability the despotic population was more successful in terms of size. But there are also differences in the results. In the condition with high predation pressure there is no significant dif-

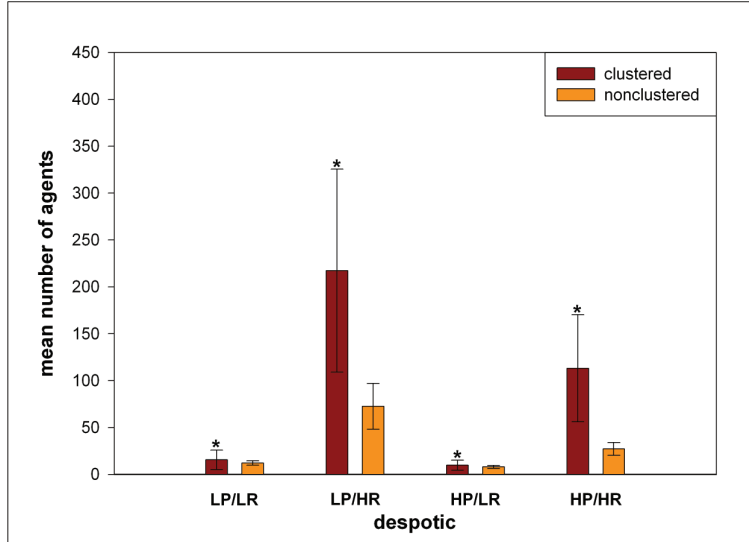


Figure 7.13: Comparison of the population size in the clustered vs. non-clustered setting for egalitarian agents

ference between the populations. In the non-clustered setting in this condition the despotic population was significantly bigger. The other difference the result of the condition with the combination of high predation pressure and low food availability. In the non-clustered setting there was no significant difference in this condition but in the clustered setting the egalitarian population was significantly bigger than the despotic population.

These differences illustrate a trend in the clustered setting. The clustering of resources into big patches makes them monopolisable on a group level. Since the clusters in the simulation are relatively big they represent an advantage for both species, because the agents don't have travel far to feed and can stay closer together to avoid predation. In the case of the results of the clustered setting this means, the strong negative effect of high predation on the egalitarian agents was counteracted by the clustering, giving them a relative advantage over the despotic agents in conditions with low or average food availability, which affected the despotic population more.

The results for the number of agents killed by predation, the number of agents died of starvation and the number of offspring are similar to the results of the non-clustered setting (appendix 12.1.1). More egalitarian agents were killed by predation and more despotic agents died of starvation. In general in all condi-

tions more offspring was produced by both of the agent groups. This increase is the result of the clustering of food resources, because the agent have to travel less far to obtain enough food in order to reacher the energy level necessary for reproduction.

### **Comparison of the results of clustered and non-clustered setting**

In the third set of results the clustered and the non-clustered setting were compared with each other. This comparison shows that both the despotic population and the egalitarian population were significantly bigger in all conditions with clustered food setting. As mentioned above the sizes of the food patches are the decisive factor for this effect. Since they are big enough to sustain a number of agents at any time they provide more food in close range for all agents in one group. They become therefore monopolisable on a group level. Compared to the non-clustered setting the agents don't have to move as far to obtain enough food from the environment and reach the necessary reproduction energy level faster. This effect is illustrated by the comparison of the results for the number of offspring in the two different populations in the different conditions and settings (appendix 12.1.1). Both the despotic agents and the egalitarian agents produced significantly more offspring in the clustered condition.

In summary it can be said that large clustered food resources are better for both agent population. They enable the agents to reach the energy level necessary for reproduction faster compared to an environment with the same amount but randomly distributed food. Combined with the effect of a relatively closer spatial structure which helps avoiding predation, clustered food resources in the model enable at least in conditions with sufficiently high food availability bigger populations. It is again necessary to point out, that these conclusions are only valid in comparison with an environment with the same amount of equally distributed food in it.

## 7.4 General discussion

There are several critical points concerning the MSI model which need to be discussed. The first point is how the differences in spatial distribution are determined. The SET argues that the different social interaction patterns observed in different primate species can be categorised into more or less egalitarian and more or less despotic. The difference between these categories is based on different parameters. In the case of the MSI model two of these parameters were chosen to implement the different types of agent populations. One parameter was spatial distribution, the other tolerance level. The SET proposes that the tolerance towards each others proximity is lower in despotic species compared to egalitarian species and that the reason for this is their closer spatial distribution. In the model the egalitarian agents have therefore a wider spatial distribution than the despotic agents and are more tolerant towards each others proximity. The parameters more dense and more wide, which are, besides tolerance towards each others proximity, the discriminative factors between egalitarian and despotic social structure in the model, do not correspond with actual empirical quantitative measures. They represent the general spatial structure of the two different social structures as described by the socio-ecological theory. The results of the model show that it is possible based on the spatial distribution described in the socio-ecological theory in interaction with predation pressure and food availability to implement a model which matches the predictions of the socio-ecological theory.

Even though the way spatial distribution is implemented in the model produced results which correspond to the predictions of the SET and can therefore be seen as a sufficient minimalistic representation of egalitarian and despotic, a more throughout analysis of the changes in the spatial structure of the groups during the simulation would be a desirable extension of the model. Such an extension would help to analyse further questions about the influence of environmental pressures on the spatial distribution of group living animals and to more adequately discuss the discrepancy between the PIT and the SET addressed in section 9.5.

While working on a spatial analysis procedure several conceptual and pragmatic problems occurred which made the implementation of the procedure at the time impractical. During the simulation especially the agent group with the more egalitarian social structure splits up into smaller subgroups which wander away from each other or merge again to one bigger group after a while. This would make

it necessary not only to analyse the distances between the agents in a group or the distance of the agents from the centre of their group, but to calculate the centre of mass for each of the subgroups and then the distance of these centres from each other additionally to the distance of each of the agents from the centre of its subgroup. By the time this problem occurred there was insufficient computational time to run the model with such a spatial distribution analysis extension. Such an extension can therefore be seen as possible future work to be done with the MSI model.

The aim of the MSI model was not to simulate the evolution of egalitarian or despotic social structures, but to compare their adaptability to certain environmental conditions. In terms of empirical research this means, the environmental conditions and the social structure of the groups are the independent variables and population size, number of agents starved, number of agents killed by predation and number of offspring are the dependent variables. It would therefore be impractical to compare the results of the model with empirical result from field work in such a way as if this model would be an empirical experiment itself. It is only possible to discuss the degree to which the results of the “simulated” SET (represented in this model) matches the assumptions and explanations of the SET.

In the MSI the social structure of the groups are fixed and cannot be changed. Hence it is not possible with the MSI to simulate how and under what circumstances different social structures could have evolved. It is only possible to test which ecological factors could have played a role during the evolution of social systems. It is also not possible due to the fixed social structures to test how stable these social structures are or how stable they would be or need to be in changing environmental conditions, in other words it is not possible to test the necessary flexibility of the social factors involved in the evolution of social structure.

These points illustrate the limitations of this model, but also show what is possible to conclude from its results. If we assume that the differences between despotic and egalitarian social structures are correctly defined in the socio-ecological theory and these definitions are correctly implemented into this model, the results show that primate species with an egalitarian social structure should be more successful in terms of population size in environments with low predation pressure and restricted food availability and more despotic primate species should on



the other hand be more successful in environments with high predation pressure and high food availability.

This corresponds to the empirical data the SET uses to define *Type B* and *Type D* environments (see section 3.4). In *Type B* environments despotic populations live in conditions with high predation pressure and a high carrying capacity of the environment. In *Type D* environments egalitarian populations live in conditions with low predation pressure and a carrying capacity which matches the group density. The clustering of food on the group level was an advantageous for both populations, but the comparison of the relative increase in population size shows that in most conditions the egalitarian population was bigger. This also corresponds with the predictions of the SET. In a *Type D* environment the clustering of food resources into large patches is more advantageous for egalitarian species.

In the model the two different agent populations were modelled in the same environment. This was done in order to monitor the behaviour of both populations in the environment at the same time which made the implementation of the model and the initially necessary parameters sweeps much easier. The parameter sweeps were necessary to find settings which enabled a stable running of the model (see section 7.2.1). The agents of the two populations were ignorant of each other and the environment was big enough for them to not influence each others behaviour. Both populations were therefore model as if they were alone in the environment. But the existence of a second population in the environment, even if does not directly interact with the first population, represents a hidden condition. But the implementation of an additional interaction possibility for the two population would have increased the complexity of the model to a large extent and at the same time decreased its comparability with the basic assumptions of the SET. Nevertheless the implementation of such an interaction between two species with different social structures could be a valuable extension of the MSI model in order to test different research questions.

Additionally to this there are different other ways the MSI model could be extended. One way is to change the fixed social structures of the species in the model into more dynamic social structures. With such a setup it would be possible to test how changes in the environment change the characteristics of inter-individual interaction patterns and therefore social structure. Another way to test which

social structure is better adapted to certain environmental conditions would be to implement one group of agents composed of individuals with different interaction patterns into different types of environments. In such a model setup the composition of the group should change according to the environmental conditions in such a way that it would contain at the end of an experimental run only individuals which were better adapted to the environment. Another possible extension would be to test the effects of food resources which are monopolisable on an individual level. In order to do so the food clusters in the model would need to be much smaller than in the MSI-step2 model. This would require an entire new parameter sweep to change the parameter settings of the model in such a way that it would run stable with very little food in the environment. All these possible extensions are an illustration of the limits of the present model, but they also show what has already been gained. The MSI model represents a working model to test the basic dynamics of the development of social structures and can be used as valuable base for many further extensions to test different and even more complex theories and research questions.

## 7.5 Conclusion

In summary the results of the MSI model can be seen as an additional argument for the consistency of the socio-ecological theory. The results give no information about the reasons for the development of different social structures, but they do help to make predictions of how a species with already established social structures like the ones described in the socio-ecological theory would be adapted to different environmental conditions. The findings of the MSI-model underline the point that a species with an inflexible social structure migrating into an environment with different conditions would have a considerable disadvantage compared to a better adapted species using the same food resources in this environment. The central statement of the socio-ecological theory is that the social behaviour of for example different macaque species is flexible and depends on the environmental conditions. The central argument of the phylogenetic inertia theory on the other hand is that especially for macaques the social interaction patterns depend on the genetic heritage and are rather fixed. There is no direct way to prove one or the other theory to be true with an agent-based model such as the one presented in this chapter. Nevertheless showing with this model that different

environmental configurations give one of two different species in the same environment an advantage over the other illustrates that it is unlikely for a certain species to maintain its social structure for a long time and still be successful in a new environment with different pressures.

# Chapter 8

## Variables influencing social dominance and female mate choice

### 8.1 Introduction

The goal of this chapter is on one hand to test the effects of various selective pressures on the evolution of social dominance and on the other to illustrate the advantages of ABM as a methodology. It represents an extension of the DIM from chapter 6 and in doing so shows that it is possible with ABM to extend an already built and working agent based model in order to explore related theories. In the DIM the plausibility of predation being the possible reason for the development of dominance behaviour was explored. The dominance behaviour in the DIM was based on the ability to displace conspecifics.

In the extension presented in this chapter the effects of sexual reproduction, female mate choice, different rates of variance in male dominance inheritance and the impact of rank fights on dominance as an indicator of male quality and the development of dominance hierarchies are tested.

## 8.2 Background

As discussed in chapter 2 dominance can be defined as the position of an individual in the hierarchy of its group. The higher the dominance of the individual the higher it is in the hierarchy. Dominance is normally correlated with priority access to food resources and potential mating partners. Fitness is usually defined as a measure for the reproductive success of an individual. In this model a theory is explored in which dominance reflects a set of attributes which contribute to fitness. This set of attributes is called “quality”. Besides social dominance other factors like facial colouration have been suggested to influence female mate choice (Waite et al., 2003). An association of this signal with male dominance status has been reported in different primate species (Setchell and Dixson, 2001; Gerald, 2001). The exact nature of signals used by primate females to choose their mating partners is still subject of further research.

Females inherit their dominance position in the hierarchy from their mothers. High ranking females will have high ranking female offspring (Silk, 2007). As a result the female dominance hierarchy can remain stable over generations (Silk, 2002). When they mature, daughters attain a rank just below their mother, and older daughters rank higher than younger daughters (Chapais, 1995). Small female juveniles can defeat larger juveniles from lower ranking matriline if their mother is around, but not if she is not.

For females, their lifetime fitness depends on their dominance position in the group. High ranking females have higher lifetime fitness than low ranking females (Silk, 2002, 1993; Cheney et al., 2004; Altmann and Alberts, 2005). Therefore any reproductive advantages dominant females accumulate will be magnified over time due to the inherited stable dominance ranks (Silk, 2007). This and the fact that females in macaque species usually remain in their natal group (Kapsalis, 2003; Silk, 2002) leads in most macaque species to the formation of matriline.

In males lifetime fitness in macaques is normally also based on dominance rank. But the dominance rank of males is largely the result of physical strength and intimidation capability which usually also depends on physical strength. One possible reason for this might be the fact that males disperse from their natal groups in order to prevent inbreeding (Kapsalis, 2003; Silk, 2002) and that they are therefore not able to rely on inherited social positions.

In males therefore dominance maybe an honest signal for quality. In females the problem is more complex. For a female it is possible to be dominant because of her inherited rank without actually having a high quality.

## 8.3 Methods

Since the model discussed here is a further extension of the *Dominance Inheritance Model* the procedures of the model are with exception of the extensions the same as the ones discussed in section 6.3. The exact variable values and the initial setup of the model shown in table 8.1 were determined with the same procedure as described in section 6.5.

### 8.3.1 Sex

The first extension is sexual reproduction. In order to implement sexual reproduction into the model it was at first necessary to introduce male and female agents. The basic principle of reproduction was the same as in the dominance inheritance model. A female agent needs to find enough food to reach the energy level necessary to reproduce. The difference is the way the offspring is produced. In the *Dominance Inheritance Model* each agent spawned an offspring once it had reached this level passing on a certain amount of energy to the offspring. Here, only the females required the threshold and depleted the energy. But in order to reproduce they also needed a male.

Another new variable called *mate choice range* determined in which distance around themselves agents look for potential partners. In the condition without female choice, which represents the control condition, the potential mating partner chosen by a female agent with the appropriate reproduction energy level was the male agent closest in its *mate choice range* with a certain predefined energy level.

The sex of the offspring was chosen randomly. Its other characteristics depended on this decision. According to the above described findings about matrilineal dominance inheritance, the dominance of female offspring differed from their

quality in such a way that their dominance was equal to the dominance of their mothers. Their quality on the other hand was calculated as a noisy mean of their mother's and father's quality (see equation 8.1). Quality represents a set of attributes associated with fitness, as described in section 8.2.

$$offspring_{female} \left[ \begin{array}{l} quality = \frac{quality_{mother} + quality_{father}}{2} + random \\ dominance = dominance_{mother} + random \end{array} \right. \quad (8.1)$$

For male offspring the quality was calculated the same way it was for female offspring but the dominance did not depend on the dominance of one of the parents but on the quality of the offspring itself (equation 8.2). In males therefore the dominance was an honest signal for quality, in females the quality was disguised by the socially acquired dominance.

$$offspring_{male} \left[ \begin{array}{l} quality = \frac{quality_{mother} + quality_{father}}{2} + random \\ dominance = quality + random \end{array} \right. \quad (8.2)$$

The next extension added was female mate choice. The difference compared to the procedure above was the way the potential partner for reproduction was chosen. The females choose in this experiment the male with the highest quality value in their *mate choice range* as partner and not the male closest to them. In Rhesus macaques for example females exhibit a high degree of choice when selecting mates (Manson, 1992). They don't choose males based on dominance rank (Manson, 1994b) or on established relationships (Manson, 1994c). This model will test the effects the selection of quality in males by females has on the overall quality and the overall dominance in the group.

Another variable tested with this configuration was a higher rate of male quality variation in the inheritance of male quality. As described above each agent inherits the characteristics of its parents. To increase the ecological validity of this process each value was inherited with a certain random variation normally distributed around 0. For this particular experiment the rates for this variance of the inherited quality in males was increased.

These experimental configurations represent the first part of this extension, since they are all closely linked to each other conceptually. The conditions with and without female mate choice were added using the same configuration as in the baseline condition. After this the model was run again with varying rates of male quality variation.

Variable	Setting
female mate choice	on or off
male variation	0 or 0.2
rank fights	on or off
hunting time	10
energy costs	4
food value	6
mate choice range	16
Perspace	6
NearView	16
MaxView	40
population size	20
predation rate	12.5
regrowth-rate	31.5
agent life time	200
reproduction costs	32
vision-radius	40

Table 8.1: Initial parameter settings for the extension of the DIM

### 8.3.2 Rank fights

The other experiments conducted with this model were a little different from the ones mentioned above. They deal more directly with the inter-individual interaction patterns of the agents. Their aim was to test the effects of rank fights on the selection for quality in the group. A rank fight in the model is a fight which has a consequence on the positions in the dominance hierarchy of the individuals involved. As mentioned in chapters 3 and 5 there is a lot of evidence



that fight outcomes can affect dominance rank. However, as shown in chapter 5 ranks derived purely from rank fights are not biological plausible.

In order to test the effects of rank fights the second part of Hemelrijk's interaction algorithm was introduced into the model. But in order to avoid the highly dynamic hierarchy structure resulting from this integration, for reasons discussed repeatedly before (section 5.7.2), only individuals which are close to each other in the dominance hierarchy engaged in fights which resulted in such rank fight outcomes.

This was established by introducing a *conflict interval*. The agents attacked all other agents intruding their personal space with an dominance value equal to their own  $\pm 1$  percent. This resulted in a much lower fighting frequency, yet also avoided rapid and unrealistic changes in the dominance hierarchy of the group.

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These experiments were run with two conditions. In one condition fights between the agents had no consequence for their position in the dominance hierarchy of the group. In the other condition the dominance values of the winner and the loser were changed according to the result of the interaction. Only the confrontation between two almost equal individuals was counted as a fight in either condition.

## 8.4 Results

During the experiments the development of the average quality and the average dominance value of the group and for male and female agents separately and the coefficient of dominance variation were measured as dependent variables. The coefficient of dominance variation represents a measure for the differentiation of the hierarchy in the group. The bigger the coefficient, the bigger are the differences in the dominance values of the individuals in the group. Additionally to these measures for the rank fights extension the number of fights was monitored.

Following the structure of the extensions of the model the results can be categorised into two different sets. The first set represents the findings related to the reproduction extension, the second set represents the findings of the rank fight extension.

### 8.4.1 Adding sexual reproduction and female choice

Figure 8.1(a) compares the average dominance value in the group in conditions with and without female mate choice. Figure 8.1(b) compares the average quality in the group for the same conditions. In the condition without female mate choice both average dominance value and average quality is relatively stable. This is due to the fact that females always choose the closest available partner not paying attention to quality. In the condition with female mate choice both the average dominance value and the average quality in the group increases due to the females always choosing the male in their mate choice range with the highest quality value. The increase in dominance is less steep then the increase in quality, because only in male offspring the quality is linked to dominance.

Figure 8.2(a) shows a comparison of the average male dominance in conditions with high male quality variance and low male quality variance. Figure 8.2(b) compares the average male quality for the same conditions. In the condition with high male quality variance both the average dominance and the average quality in males increases faster compared to the condition with relatively low variance.

The results for average female dominance and quality show a different structure.

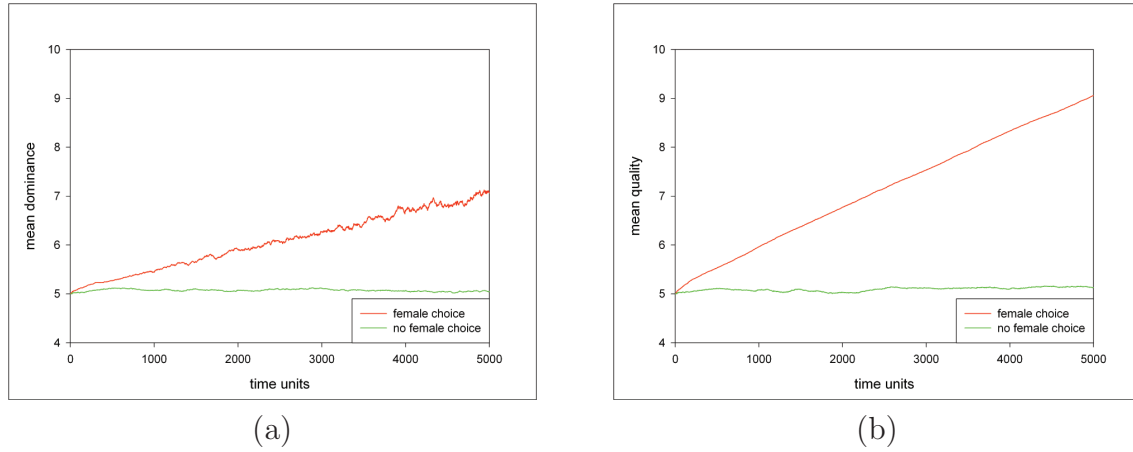


Figure 8.1: Average dominance value (a) and average quality (b) in the population in conditions with and without female mate choice

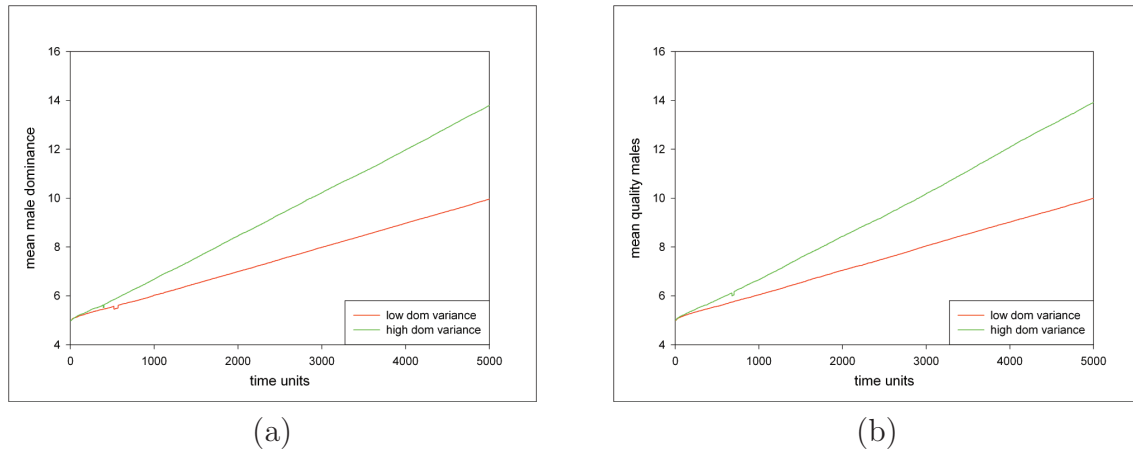


Figure 8.2: Average dominance (a) and quality (b) in males with varying levels of male quality

The average female quality shows the same structure for both conditions like the male quality structure (Figure 8.3(b)). The female average dominance however decrease in both conditions initially, but then increase in the condition with low male quality variance and stabilises at a higher value compared to the condition with high male quality variance (Figure 8.3(a)).

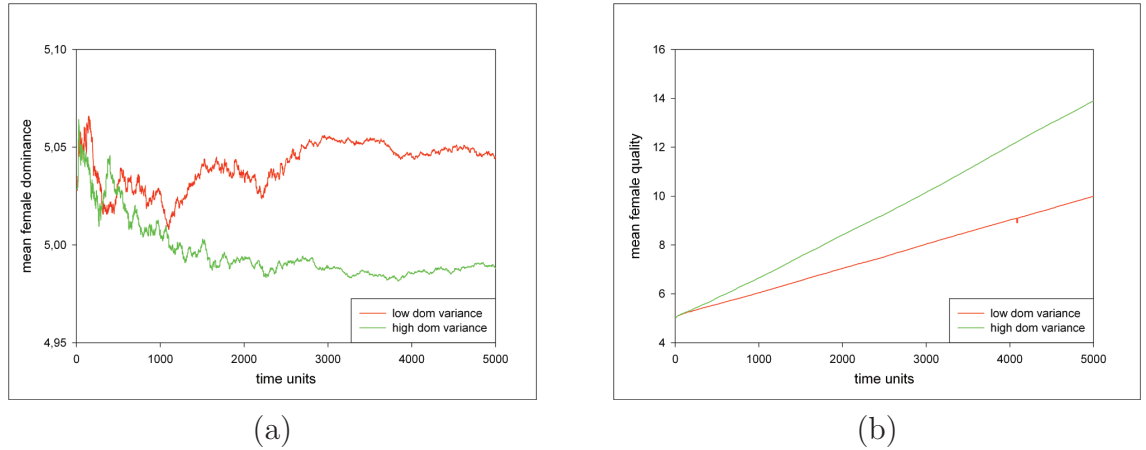


Figure 8.3: Average dominance (a) and quality (b) in females with varying levels of male quality

### 8.4.2 Adding rank fights

Figure 8.4(a) shows that the average dominance in the group increases more than the average quality in the condition in which the outcome of fights had an influence on the dominance hierarchy. Figure 8.4(b) compares overall dominance and quality in the condition in which the outcome of fights had no influence on the dominance hierarchy. Here the increase in quality is higher than the increase in dominance.

Figure 8.5 compares the number of fights in the experimental conditions. The number of fights was smaller in the condition in which their outcome changed the dominance value of the participating agents.

### 8.4.3 Coefficient of dominance variation

Figure 8.6(a) (page 138) shows the development of the coefficient of dominance variation for conditions with and without female mate choice. In the condition without female mate choice the coefficient stays very low indicating small differences in the individual dominance values. The opposite is true for the condition with female mate choice. Here the coefficient increases indicating more and more differentiation of the dominance values in the group. In figure 8.6(b) (page 138) the development of the coefficient of variation for the conditions with high and

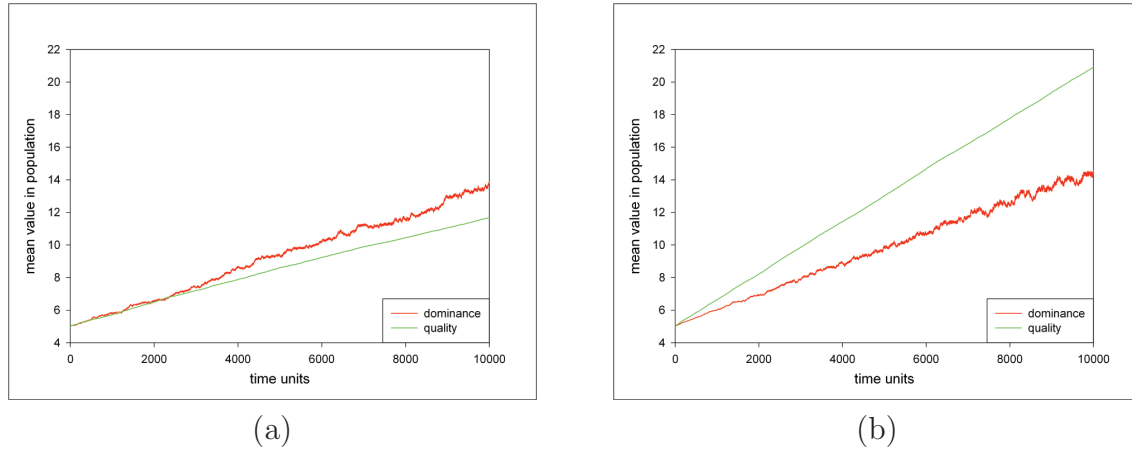


Figure 8.4: Comparison of population dominance and quality for the condition in which the outcome of the aggressive interactions had an impact on social dominance (a) and for the condition in which they didn't (b)

with low male variation is compared. It shows a steeper increase of the coefficient in the condition with high male variation. Figure 8.6 (also on page 138) compares the coefficient of dominance variation in the conditions with and without rank fights. In the condition with rank fights the coefficient increases faster, but also stabilises quicker compared to the condition without rank fights.

## 8.5 Discussion

The model discussed in this chapter illustrates one of the advantages of ABM. Once a working model is established it can be modified and used as base for new models in order to answer different questions. It is possible by adding one new variable after another to test different theories. In the case of the model in this chapter the DIM from chapter 6 was used as base and then its complexity was increased by adding different parameters to it. By doing so the model produced a series of results which can help to understand the influence of different social factors on the evolution of social dominance and social hierarchies.

The first result to be discussed is the effect female mate choice has on the average dominance and male quality in the group. As mentioned in section 8.2 in the model quality is defined as a set of attributes related to fitness and dominance as the ability to displace conspecifics. Both parameters are in the experimental runs

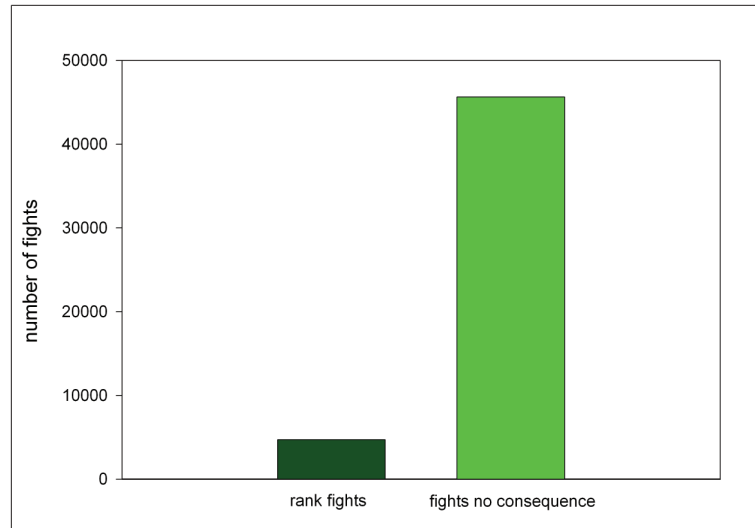


Figure 8.5: Comparison of the overall number of fights in the conditions in which the outcome of aggressive interactions had an influence on the dominance hierarchy (rank fights) and in which they didn't

the dependent variables. In the case of male quality the difficulty of its operationalisation is that it is not yet entirely clear which exact signals female primates for example use to judge the fitness of potential mates. Therefore quality in the model has to be seen as a “summary” variable for attributes related to fitness and was chosen to represent a variety of potential signals. Dominance on the other hand was, like in the DIM, operationalised as the ability to displace conspecifics after dominance interactions. The problem with this operationalisation is that there is no clear phenotypic differentiation between different dominance levels in reality. Although in the context of the model it is possible to measure after 10 generations a higher level of dominance (mean dominance value), the behavioural effects stay the same: a dominant individual displaces a subordinate individual. For observational research the mean dominance value in the group plays a secondary role because its changes would only become visible over long periods of time and many generations. The mean dominance value should therefore be seen as a long term measure for the group internal selection pressure to displace others. This selection pressure could lead to a variety of different effects, ranging from an increase in body to more cognitive functions like the ability to form coalitions.

The first results of this extension of the DIM shows that adding female mate choice into the model increases both the average dominance and the average

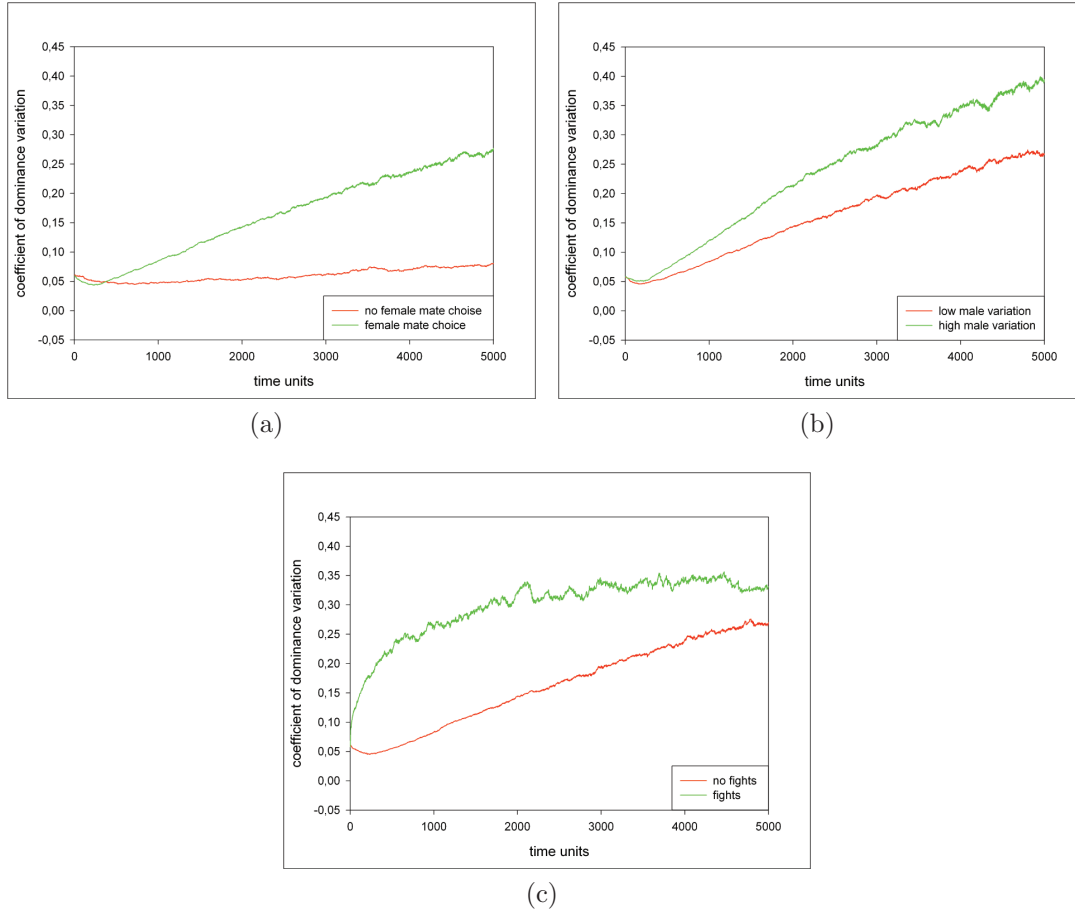


Figure 8.6: Comparison of the development of the coefficient of dominance variation as measure of hierarchy differentiation in conditions with and without female mate choice (a), high and low male quality variation (b) and with or without rank fights (c)

quality in the group (see figure 8.1). In the female mate choice condition females always choose the males with the highest quality value in their vicinity for reproduction. Dominance in males is directly connected to their quality and the quality of the father is passed on to the male offspring. This results in an increase of the average quality, and to a lesser extent of the average dominance value in the group. Based on these results it could be argued that a mechanism based on the selection of certain traits which signal fitness in males, like female mate choice, leads to an increase of the average quality and the average dominance value in the group. This sounds simple, but it has to be interpreted on the background of the results of the DIM, which are the base for these extensions. The results of the DIM showed that predation could be the initial reason for the evolution of gregariousness and social dominance. Once group living had evolved other mechanisms could have evolved and accelerated the development of social dominance

hierarchies. Female mate choice could have been one of these mechanisms. This becomes more obvious in the result shown in figure 8.6(a). Here the comparison of the development of the coefficient of dominance variation in the conditions with and without female mate shows an increase of the coefficient if females choose their mating partner based on a variety of signals related to fitness. This increase means that in the model the development of the dominance hierarchy is initiated by female mate choice, because in the condition without female mate choice the coefficient is stable, meaning no differentiation between the agents in dominance.

Another additional influence in the process of hierarchy differentiation could have been genetically induced rates of male variation. The results in figure 8.2 show that both the average dominance and the average quality in males increases if the variance in inherited quality in males is increased. Due to female mate choice, the more dominant males are chosen for reproduction. More variance means that the maximum and minimum value of male quality in the model are further apart from each other. Since male quality is directly linked to their dominance and females choose the male with the highest quality value to reproduce and the quality value of the male is passed on to male offspring, the average dominance value in the condition with high variance increases faster compared with the average dominance value in the condition with low male quality variance. Figure 8.3 shows that the average quality of females increases the same way as the quality increases in males. Since the quality of the offspring is calculated the same as in males, the offspring inherits 50% of the mother and 50% of the father, this result is not surprising. Due to the selection for higher quality and with it for higher dominance in males by female mate choice the increase in quality is amplified over time. The result for female dominance however can be explained by the independence of dominance in females from males. Female offspring inherit the dominance value of their mother not from the father. The result of high variance in male quality is an decrease of female dominance. For low male quality variance the female dominance fluctuates initially but stay on the same level. One possibility to explain this effect is the ability of dominant males to displace subdominant females. The higher this ability, the more negative the influence on female dominance. In other words the average female dominance is suppressed by very high dominance in males. Since the effect of high variance in male quality is a stronger selection for dominance in males due to female mate choice, the result is a lower average dominance level in females.



These results become more clear when comparing them with the results for the development of the coefficient of dominance variation for the different rates of male quality variation. These show that male quality variation is an additional factor in the process of hierarchy differentiation in the model. In both conditions, high and low male quality variation, female mates choice was “turned on”. This led to a differentiation of a dominance hierarchy. The condition with low male variation is comparable with the female mate choice condition and accordingly shows a similar result for the coefficient of dominance variation. The differentiation of the dominance values is even stronger with high rates of male quality variation, meaning that the higher variation had an additional effect on the development of the groups dominance hierarchy. These results show that as an side effect different rates male quality could have accelerated the development of dominance hierarchies.

The second part of the results deals with the influence of rank fights between individuals with a similar dominance level on the average dominance value and average quality in the group. If dominance can vary independently of quality after birth, then it can have other additional roles besides allowing the highest quality individuals priority access to resources. If we assume that males with similar ranks are more likely to risk injury in fights, then allowing fight outcomes to influence rank (and female mate choice) reduces risk of injury at the cost of compromising (but not eliminating) selection for quality-associated traits. Figure 8.4 shows that if fight outcome has an influence on rank the average dominance in the population is larger than the quality, if it doesn't the average quality in the population is larger than the average dominance.

The result shown in figure 8.5 and the results for the coefficient of dominance variation (Figure 8.6(c)) both illustrate the stabilising influence of rank fights like the ones implemented in this model on the dominance hierarchy of the group. The result for the number of rank fights (figure 8.5) shows the that conflict falls off quickly when small differences in rank can be adjusted through fights. The number of fights is much smaller if their outcome has an influence on the rank of the involved agents. The results of figure 8.6(c) show that the increase in dominance variation in the group is much steeper in the beginning of the simulation and that it starts to reach a stable point faster in the condition in which the outcome of the rank fights had an influence, whereas in the condition in which the rank fights had no influence the coefficient of dominance variation

increases constantly. Since in the rank fight condition dominance interactions only take place between individuals with dominance values close to each other (enabling the winner to shift rank), an increase in differences in dominance values makes the hierarchy more stable by decreasing the possibility of the individuals in the group to encounter each other in dominance interactions. This on the other hand also accelerates the development of a dominance hierarchy in a social group.

## 8.6 Conclusion

The results of the extensions of the DIM show in summary that if we assume that social interactions are influenced by environmental factors like predation and food availability and by the resulting spatial structure in the group that there is a selective pressure towards hierarchical dominance structures. From the perspective of the model, social dominance is the ability to displace other individuals and serves in an environment with predation as assurance to maintain a central position in the group and be therefore protected from predation. Even if social dominance is more complex than this, the results concerning female mate choice and male variation still hold. Female mate choice as well as a bigger variance in male quality promote the selection towards bigger overall dominance in the group and towards a differentiated social dominance hierarchy given a matrilineal transmission of female dominance.

The results for the condition with rank fights show that if aggressive interactions between equally dominant individuals have an influence on the dominance hierarchy then the average dominance increases more than the average quality. Also the number of fights decreases if their outcome has an influence. These two results allow the conclusion that conflict resolution in such a way that the dominance hierarchy is influenced by fights between equal individuals leads to an increase of dominance in the population but not necessarily of quality in the same way. If there are no consequential fights the selection towards dominance in the model is less strong and the selection for quality is more pronounced. The reduced frequency in the number of fights in the rank fight condition can be explained by a stronger segregation of the dominance values of the agents due to the influence of the fights. The distance in rank between the agents is represented

by the difference in their dominance values. Agents engage only in fights with agents of similar dominance value. If agents start to win and others to lose the differences their dominance values will increase and they will stop fighting each other. This will eventually lead to an established hierarchical dominance structure. This conclusion is also supported by the results for the coefficient of dominance variation.

# Chapter 9

## Discussion of Social Structure

As mentioned in section 1.3 this thesis has two different research questions.

1. Is it possible to test the coherence of the different existing theories about how environmental pressures influence the evolution of social dominance and social structure with working agent based models?
2. How can agent-based models as technological tools help behavioural researches to find answers in the field of social evolution? What are the potentials and what are the restriction of such models?

The second question has been partly answered in chapter 4. A thoroughly answer to this research question will be given in chapter 10. In this chapter the results of the different models discussed in this dissertation will be summarised and related to the first research question, starting with the replication of DomWorld.

### 9.1 Models about the evolution of social dominance and social structure

I started to answer the first research question by analysing and replicating the only agent based modelling environment which had been implemented so far and

dealt with the possible reasons for the evolution of different social structures in primates. The replication of this modelling environment called DomWorld enabled a critical analysis of the assumptions it is based on and of the way the different interacting variables, which its dynamics are composed of were implemented.

In a next step an agent based model based on the most basic theory about the reasons for the evolution of gregarious life style in animals by Hamilton (Hamilton, 1971) was implemented. This **Dominance Inheritance Model** uses two environmental pressures (predation and food availability) and genetic random variation to answer the question whether predation pressure could have been the initial reason for the evolution of social dominance. By including genetic random variation, the model also includes assumptions from the **Phylogenetic Inertia Theory** (Thierry, 2006) about the influence of genetic drift on social structure, because the offspring in the model inherits the dominance characteristics of its parent.

After examining the results of the DIM I focused on the **Socio-Ecological Theory**. The SET postulates that environmental pressures are the main factor influencing social behaviour in non-human primates and that changes in the environment shape the way individuals in different primate species interact with each other, resulting in either a more despotic or more egalitarian social structure (van Schaik, 1989). Its main opposing theory is the PIT. The PIT postulates that differences in non-human primate social structure are mainly based on genetic heritage. According to Thierry (2007) environmental changes can alter the way behaviour is expressed, but their influence is only secondary to the genetic background of a species.

In a last step I extended the DIM by implementing other factors possibly influencing the evolution social dominance and social structure. These other factors are female mate choice, different rates of variation in male quality and rank fights between individual close in the dominance hierarchy of the group.

As discussed in chapter 4 and chapter 10, modelling can never be a substitute for empirical evidence. Thus none of the results of the models in this thesis should be treated as proof for the empirical content of the theories they deal with. The fundamental function of each of these models is not to prove the truth of one theory, but to test their theoretical coherence. This theoretical coherence is a

precondition for the empirical truth of a theory, specially if the subject of the theory is an emergent phenomenon like the evolution of social organisation.

The operationalisation of variables is of central importance both for good modelling and for good theory building : “How are the phenomena a theory wants to explain made measurable?”. Different types of operationalization lead to different explanations. Hemelrijk’s results and the replication of her DomWorld are a good example for this. Hemelrijk’s main variable is the dominance value. It combines the operationalization of two phenomena: hierarchy and social interaction. In this case one variable describes two main elements of a theory.

## 9.2 Replication of Hemelrijk’s Domworld

In Hemelrijk’s model the dominance value of an individual is connected to its probability to win a fight. This value increases with victory and decreases with defeat. If an individual wins against an individual with a much higher dominance level, the dominance value increases much more than in the case of winning against an individual with a lower level. These are the basic dynamics of DomWorld.

DomWorld uses also a specific operationalization to model the different social styles. It differentiates the different types of primate societies by the level of aggression in a single dominance interaction. Aggression is operationalised as a variable called *StepDom*. The higher *StepDom* the bigger the extent of the change of the dominance values after an interaction. Therefore in her model being egalitarian is characterised by a low *StepDom* and being despotic by a high *StepDom* value. After implementing these principles into a model it was possible to replicate her results.

In her model different types of social structure are operationalised as different levels of *StepDom*. The consequence from this is that higher levels of aggression lead to a higher variance between the dominance values of the individuals. By itself this is only a description of the self-reinforcing effect of dominance. But in combination with the additional factor of female attraction this model offers a possibility to visualise how emergent effects like male tolerance or female assert-

iveness may evolve. Females become able to outrank males in conditions with high levels of aggression, but on average no more than 50%. Really high StepDom values just randomise the result. This effect additionally increases the variance between the dominance values of the individuals. One interaction effect is that the increase of dominance in females depends more strongly on attraction than on aggression. This attraction leads to a higher interaction frequency which in turn leads to more changes in the dominance hierarchy and increases the probability for low ranking individuals to win.

DomWorld is not a complete representation of the SET, because it does not include environmental factors influencing the behaviour of the agents. Hemelrijk's theory is more in accordance with the boundary conditions of the PIT. DomWorld represents a snapshot of her theory showing a proximate account of behaviour. It does not answer the question of how and under what environmental conditions social dominance could have been adaptive. It is more an attempted demonstration that increased violence in interactions is a sufficient explanation to account for all social structure differences.

My main criticism of her model is the way she implements social hierarchies. In her model they are highly dynamic and individuals can move up and down in their hierarchy quite easily. After checking with the relevant literature this seems incorrect (Thierry, 1990, 2006; van Noordwijk and van Schaik, 2004). In most primate species social hierarchies are stable and it is unknown for a low ranking individual to defeat a very dominant member of its group. Thus the fact that just by increasing the interaction frequency the probability for low ranking individuals to win against a very dominant group member increases seems to be very unlikely.

During the replication of her work different problems with the way Hemelrijk implemented some of the variables she wanted to examine became visible and lead to a critique of DomWorld (Lehmann et al., 2005). Also the lack of documentation and availability of the model code occurred as a major obstacle in the replication of her work. In order to improve ABM as technology for social science it is desirable to be methodologically clean and provide the code including a documentation for other researchers online.

But despite all the criticism Hemelrijk has made a major contribution to the

field of agent based modelling. Replicating DomWorld helped to understand the dynamics of agent based models and to specify the questions I wanted to answer with my own models. Some of the parts of her model, like the idea of the mental battle, implemented as first part of her interaction algorithm, and the use of the three vision variables PerSpace, NearView and MaxView are very useful. This is the reason why I applied them in my models. This by itself shows the possibilities of ABM specially in the development of new scientific theories. Modifying and extending existing models in order to test different ideas becomes possible. This process helps us to create better and better ABM tools for the examination of scientific theories.

### 9.3 The dominance inheritance model

The DIM represent an implementation of the theory by Hamilton (1971) about the initial reasons for the evolution of social dominance. It tests the effects of predation pressure and food availability on the evolution of social dominance. Predation pressure was implemented in the model as the cohesive force, food availability as a force driving the agents apart and social dominance as the ability to displace other individuals. The higher the dominance value of an agent was, the higher was the probability for the agent to win a dominance interaction.

As shown in section 6.4, the average dominance value in the group increases if dominant individuals have the ability to displace subordinate individuals. As result dominant individuals occupy the space in the centre of the group. The result of the control condition shows that if winning a fight has no spatial consequences, then dominance has no selective advantage.

The reasons for the existence of dominance have been widely discussed. Usually in most gregarious species the dominant individuals are under a lot of stress (Creel, 2001). They have to be alert most of the time to protect their position and their priority to resources (Chance, 1967). In some species this even leads to a higher vulnerability of dominant individuals to parasites and to a shorter lifespan (Gage, 1998). But even though dominance is related to these disadvantages, the fact that dominance hierarchies do exist in a lot of species shows that it must also pay off for an individual to be dominant. The results of the model show an



increase in average dominance in conditions in which dominant individuals are able to displace the subordinate individuals in an environment with relatively high predation pressure.

Being dominant seems to pay off only if it gives the individual priority access to resources. In the dominance inheritance model the resource is the central space in the group. In conditions in which the dominant individuals chase the subordinates to the fringe of the group there is a selection pressure towards dominance because the probability to get eaten is much higher at the fringe than in the centre of the group. The dominance inheritance model can be seen as successful implementation of Hamilton's theory and shows how the environmental factors described by him combined with random variation in dominance values of the agents can lead to selection towards dominance.

The DIM is, as all models are (see chapter 10), a simplification and abstraction of the real world and the complexity of social evolution. It therefore only looks at some variables which might have had an influence on the evolution of social structure. But since it "only" wants to explore whether predation could have been the initial reason for the evolution of social dominance and its results show under which circumstances this could have been the case, it can be said that it represents the variables involved in the problem sufficient enough to achieve its purpose. The model is supposed to be the base for a variety of other models and therefore more complexity can always be added to it. Nevertheless the principle of parsimony dictates to favour always the simplest solution when thinking about a complex problem. Too many implemented variables would make the results of a model hard if not impossible to interpret.

## 9.4 MSI model

The MSI model focuses on testing the central assumptions and predictions of SET. It tests whether it is possible to generate a coherent model based on its basic assumptions, which produces results that fit the predictions of the theory and the empirical data.

Essentially the SET states that changes in the habitat of a species can change

individual social interaction patterns through selection. Depending on the environmental condition, the social style of a species living in these conditions would be predictable. As discussed in chapter 3 and shown in Table 3.3 the main environmental pressures in SET are predation, food distribution and food availability.

The *MSI model* is separated into two phases in order to minimise the complexity of its results and enable a meaningful interpretation. Having three independent variables interacting with each other in phase two creates different interaction effects within the structure of the model. Another reason for explaining the model in two phases is to illustrate good ABM. Adding one variable after another is important to handle the complexity of the problem and to understand the interactions executed by the agents in the model.

The four dependent variables measured in the model were population size, number of offspring, number of agents starved and number of agents killed by predation. The fitness of a group was operationalised as population size and represents the central result of the experiment. The other three variables were measured in order to be able interpret the population size results better.

As discussed in section 3.5 the SET and the PIT disagree about the average distance between the individuals in different social groups. The assumption of the SET is that despotics are closer together because they are “pressed together” by predation. The assumption of the PIT that individuals in despotic species being further apart from each other is based on the observation that the subordinates avoid confrontations with the dominant individuals (Thierry, 1986b, 1990).

In the MSI model the assumptions of the SET about the spatial distribution and Hamilton’s hypotheses were used. The SET predicts two types of environment in which despotic or egalitarian agents can be found and which are relevant for genus *macaca*. Despotic group structure should be found in conditions with high predation and a carrying capacity of the environment which is bigger than the population, corresponding with **Type B** of Table 3.3 (Vahl et al., 2005; Isbell and Young, 2002; Scott and Lockard, 2006). Examples for this condition are *macaca mulatta* and *macaca fascicularis*. Egalitarian agents should be found in conditions with low predation pressure, just sufficient food which is clumped on a group level, corresponding with **Type D** of Table 3.3 (Sterck et al., 1997; Riley, 2007). Examples for this condition are *macaca nigra* and *macaca tonkeana*.

The result of the model confirm the predictions of the SET. The wider the average spatial distribution of a group, the stronger is the negative effect of predation. In conditions with high predation and high food availability the average group size of despotic agents is bigger compared to the egalitarian agents. In conditions with low predation pressure and high or low food availability the average group size of the egalitarians agents is bigger. In the second set of experiments the food in the model is clumped on a group level or evenly distributed throughout the environment. The clumping gives both species an advantage compared to the evenly distributed food condition, because the agents don't have to move far to obtain food from the environment and because of this they can also stay closer together which gives them additional protection from predation.

But a comparison of the increase in group size of both population showed that in most conditions the number of egalitarian agents increased more compared to the despotic agents. This also corresponds with the predictions of the SET. Environments with on group level clumped food resources facilitate the development of more egalitarian species (*Type D* environment). In the model the reason for this was probably that the egalitarian agents tolerate agents closer to them and that this way they can benefit from sharing a food patch. This closeness was a result of the implementation of a compromise model between SET and PIT in which the personal space of the egalitarian agents is smaller than the personal space of the despotic agents but the average distance is bigger.

In summary it can be said that the results of the MSI model largely correspond with the empirical findings the SET is based on. The MSI model can therefore be seen as successful implementation of the SET proving the coherence of the theory especially for its conclusions about the spatial distribution of the different social structures.

Nevertheless it is possible, that the discrepancy between the SET and the PIT concerning the spatial distribution in different social structures is the result of different definitions of the same observed phenomenon. The avoidance of close proximity to other group members in despotic social groups generates the effect, that while observing such a despotic group, the animals seem to be further away from each other than they seem to be in an egalitarian group. But this effect does not necessarily contradict the assumptions of the SET about the more dense spatial distribution in despotic social groups. In the SET it seems the cohesion

of a group is meant by average spatial distribution. It is possible that on first sight, in a group with an egalitarian social structure individuals seem to be closer together, because they are engaged in more direct physical affiliative interactions with each other. But this does not keep them from also wandering around in their surroundings when foraging and leaving the centre of their group and resulting in a less cohesive group structure on average.

## 9.5 Controversy between the PIT and the SET

One of the underlying questions of this dissertation is based on the discrepancies between the PIT and the SET. Both theories show differences already in their approach, even though they are both based on observations of the same subject. By starting to operationalise the same phenomenon in two different ways, the concluding explanations of the two theories are very different. How did ABM as a scientific method contribute to the clarification which of the two explanations is correct without having an empirical decisive criterion on its own?

As discussed in section 10.2 scientific models can only test the coherence, but not the empirical validity of a theory. But the coherence is a precondition for the validity of a theory. The results of the MSI-model showed that the SET is coherent with the data in its assumption and predictions.

It is on the other hand possible to argue that the DIM represents, besides the general ideas of Hamilton about the reasons for the evolution of social dominance, also a reproduction of the general idea of the PIT about genetic drift as the reason for the existence of different forms of social structures. In the DIM the reason for changes in the overall dominance in the group is the transmission of the dominance value of the parent to the offspring. The result is an increase in overall dominance in certain environmental conditions, because more dominant individuals have a selective advantage under these condition. This statement is not given explicitly in the PIT, but it is a necessary consequence of it. If different forms of social structure are the result of genetic drift then the results of this process must have been influenced by the surrounding conditions.

The basic assumption for the explanation of genetic drift is that any cumulative

occurrence of a characteristic in a population is based on selection mechanism of this characteristic. Wright (1978) has also argued that the distribution of genes via random loss or acquisition of non adaptive alleles within a population could represent an additional evolutionary factor. The concept of genetic drift is based on the assumption that the composition of the gene frequency of the offspring generation varies from the one of the parent generation due to constant statistical fluctuation. If the absolute size of a population changes, then the relative size of these fluctuations changes as well. This means that if a population shrinks to a small size and then grows again, genetic drift can lead to more immediate changes in the gene frequency than natural selection, because the impact of natural selection happens over a longer period of time. Genetic drift has more influence, the smaller the population is. The selection mechanism is the mechanism of systematic change in evolution which determines the direction. Genetic drift on the other hand is more random. But even this randomness is constrained by a previous selection of a robust genome (Thierry, 2007). Thus even this change is systematic in that related traits adjust themselves to the change.

Both evolutionary factors, selection and genetic drift, are the basic principles of the DIM. In the model genetic drift is represented in such a way that every individual passes its dominance value on to its offspring, and that these inherited dominance values in the offspring generation can differ to a certain percentage from the parent generation. The selection of these dominance values becomes therefore visible, if they evolve in one direction or the other.

If the results of the DIM are interpreted from the perspective that the DIM is also a representation of the basic ideas of the PIT, then at this point the incoherence of the PIT becomes evident. It does not describe how the genetic drift led to different forms of social behaviour. Genetic variation can only occur on an individual level. Variation on a population level can only include a directed development, if the characteristics or behaviours connected to them are selected. Thierry (2007) has argued in this more recent article that genetic drift by itself is not enough to explain different social structures, but keeps still at the position that it plays the major role in the process of social structure differentiation.

In general selection needs not only an environment but also variation to select between. PIT explains why there are only limited forms of variation so that

despotism has similar characteristics where it has emerged. The SET explains why new species were in some cases able to outcompete older species. Both theories explain the same phenomenon from a different perspective and both theories together explain the existence of different social structures in the genus *macaca*.

## 9.6 Extensions of the DIM

The extensions of the DIM have two different functions. On one hand they test the effects of female mate choice, different rates of variation in male quality and rank fights on the evolution of dominance hierarchies and on the other it gives an example of how ABM should be used in the scientific process.

### 9.6.1 Possible factors facilitating the evolution of dominance hierarchies

The DIM only tested whether predation could have been the initial reason for the evolution of social dominance, social dominance being defined as the ability to displace other individuals. With the extensions I wanted to test which mechanism could lead to a differentiation of the dominance values and therefore to the evolution of social hierarchies. As first possible mechanism female mate choice was added to the model. In order to do so different changes had to be made to the DIM. First sexual reproduction was implemented and second the dominance inheritance algorithm was changed in such a way that it reflected matrilineal dominance inheritance. This means that female offspring in the model inherits its dominance characteristics only from the mother and male offspring inherits its dominance characteristics equally from both parents. After this female mate choice was implemented. If female agents reached the energy level necessary for reproduction, they choose the male agent with the highest quality in their mate choice range as mating partner. The results show that by adding female mate choice the average dominance value in the group increases and the dominance values start to differentiate. By adding additionally to female mate choice high levels of variation in male quality to the model this effects is amplified.

Based on these results it could be argued that a selection mechanism like female mate choice could commence a differentiation process of certain traits of the individuals in a group. If these traits are linked to the ability to displace other individuals, then this process would over generations lead to the evolution of the propensity within a species to form a dominance hierarchy. If additionally to this the variation of traits being related to or signalling fitness in males is increased due to genetic random variation in such a scenario, then this differentiation process would be accelerated.

The rank fight extension of the DIM dealt with the possible role dominance interactions between individuals, which are close to each other in the dominance hierarchy of their group, could play in the development of dominance hierarchies. The results of this extension show that if the outcome of such interactions has an influence on the ranks of the individuals then the number of dominance interaction is much lower compared to the condition in which the outcome had no influence. They also show that in the beginning of the simulation the differentiation of the dominance values increases more quickly and that the coefficient of dominance variation reaches a stable value faster in the condition in which the outcome of the dominance interactions had an influence on the rank of the individuals involved in them. Both of these results suggest that this form of rank fights could have a stabilising effect in the process dominance hierarchy formation. In terms of the model this means their outcome increases the distances between the dominance values of the individuals. In real world terms this could mean that the fight outcomes could serve as a form of conflict resolution and by that decrease the probability to get hurt in the population during the process of hierarchy formation because they help they individuals to establish their ranks faster.

Quality as variable in the model is an abstraction for a variety of traits related to fitness. In the model it not only represents fitness, which is usually measured in biology by the reproductive success of an individual, but also other variables which might have an influence on female mate choice. Since the question to be answered with the model was not which characteristics are decisive in males for being chosen as mating partner by females, but how a selection mechanism like female mate choice in matrilineal groups influences the dominance structure of the group in general, the different characteristics possibly having an influence were summarised into one variable. This is a simplification the problem, but makes

it also more manageable. Most of the results of the extension of the DIM show therefore simplified relationships, but especially the results for the development of the dominance hierarchy hold, because they can be seen as confirmation and extension of the result of the DIM and MSI models and the theories behind them.

## 9.7 Summary

The models discussed in this work represent examples for the implementation of agent based models in the field of social evolution. Their results show that it is possible to use ABM to test the coherence of different existing theories about how environmental pressures influence the evolution of social dominance and social structure. Nevertheless there are limitations to the applicability of ABM this field. These limitations have their origin in the characteristics of models in general. Models are simplifications and abstractions of reality and can never be a substitute for empirical experiments. They are aiding tools in the process of finding new or adjusting existing theories. The problems related to these characteristics and the second research question (see beginning of this chapter) will be discussed in detail in the next chapter.





# Chapter 10

## The role of ABM in social science

In the previous section the models used in this dissertation were discussed as examples for the application of ABM in behavioural science. As mentioned before simulations are not a substitute for empirical research (DiPaolo et al., 2000). The observation of expressed behaviour is the only possibility to obtain evidence about the differences and similarities of social behaviour in primates. This might be one reason why behavioural scientist are sceptical about the use of ABM in their field. But it is also important to understand that there is an essential difference between an empirical observation and an explanation (Achinstein, 1993). It is not possible to obtain empirical evidence without a theoretically grounded question, which is the reference framework for any empirical observation (Glaser and Strauss, 1967). In order to answer one of the research questions of this dissertation: “How can ABM as technological tools help us to find answers in the field of social evolution?” it seems necessary to have a detailed look at the process of theory construction and its philosophical implications and to examine the concept of modelling in science more closely.

In the first part of this chapter the differences and similarities between empirical research and modelling will be discussed from a philosophical perspective. This will be done by means of different examples from the history of science and by reviewing the process of theory construction in science. The function of modelling within this process will be shown.

In the second part of this section the problems of integrating ABM into behavi-

oural research will be discussed from the perspective of the experiences with this technology in this dissertation. At the end, ways in which ABM is a contribution to the scientific process different from empirical observations like experiments will be given. But at first modelling will be discussed from a philosophical perspective.

## 10.1 Philosophical background of modelling

In order to understand why modelling is an important part of the scientific process with explanatory value it is necessary to discuss the concept of an explanation as a starting point of epistemology.

### 10.1.1 Categorisation as the first part of explanation

The process of science can be described as finding the best explanation for a specific phenomenon in nature (Toulmin, 1965). But how can we determine what makes one explanation better than another?

At first a clear definition for what an explanation is and for the quality of an explanation is needed. Each explanation includes an *explanandum* — the object of the explanation. But the selection of an *explanandum* includes already unproven assumptions about the nature of the phenomenon in question (Sintonen, 2003; Niiniluoto, 1999). To explain the phenomenon of gravity for example, it is necessary to have an idea of what we mean by using this word. Any explanation starts with the selection of the phenomenon we choose to explain. But this selection process is subjective, because we are only able to choose phenomena which are subject to our perception and our perception is always based on presumptions (Nietzsche, 1887).

Kant (1787) showed that we can not meaningfully conceive of an object that exists outside of time and has no spatial components and isn't structured in accordance with the categories of our capabilities of understanding, such as substance and causality. Although we cannot conceive of such an object, he argues that there is no way of showing that such an object does not exist.

Already the selection of a specific phenomenon to observe is the first step towards its explanation, because by selecting it we need to differentiate the phenomenon from others (Newton-Smith, 1987). But any differentiation is based on the recognition of differences and similarities and these depend always on the perspective of the observer (Coley et al., 2004). This selection process is called *categorisation* (Medin et al., 2003; Medin and Rips, 2005).

Humans have an internal capability to categorise the phenomena they are confronted with in their environment. This capability originates in the need to make predictions about the processes we encounter in our surroundings (Erickson and Kruschke, 1998). The ability to make reliable predictions is vital for the survival of any complex organism. If members of a species are able to predict future events in their environment they will be able to adapt their behaviour accordingly in advance and therefore avoid potential dangers like predators (Barrett, 2005). In order to be able to categorise the complexity of nature we need to be able to recognise reoccurring patterns as well as differences and commonalities in the phenomena we encounter. The goal of any scientific description of our environment is a more and more precise categorisation of nature. A better and better categorisation of nature increases the accuracy of our predictions (Popper, 1982). The process of categorisation is dynamic because the way we organise our categories as well as the way we define new categories includes a certain perspective on the subjects we want to describe (Murphy and Ross, 1994; Gelman, 1988).

### **10.1.2 The role of categorisation in scientific understanding**

How the process of a more precise categorisation helps us to better understand nature is best explained by using an example from animal taxonomy. Over centuries whales were seen as fish, because they were categorised by the way they look and by the habitat they live in. For example, although Linnaeus wrongly classified whales as fishes in his original *Systema Naturae*, but eventually classified them as mammals in the tenth edition of the same book (Linnaeus, 1758). Due to a better knowledge of their anatomy and their behaviour the way we categorise them changed. Now we use the similarities in anatomy and the way

whales reproduce as defining characteristic for the categories we place them in. With more accurate data the evolutionary relationships among cetaceans and to other mammal species become clear. This example illustrates how different the categories we use to describe and understand our surroundings are. Furthermore it shows that even our scientific understanding of nature can be quite wrong and that a better understanding requires systematic testing and careful observation.

The amount of observed information changes our categorisation system. In terms of the example we have to ask the question: “What has changed in this process of finding another categorisation, our perception of whales or our explanation of what whales are?” Our perception changes the same way our explanation of this perception changes in the process of finding inconsistencies in our former categorisation. Nevertheless we still commonly use outdated concepts in our language. Saying “the sun rises” for example implies a constant position of our earth and a movement of the sun.

Not only our observations form our explanation, but also our explanation determines our perception. Every observation includes already an explanation. There is no possibility of a neutral observation without an explanatory point of view. One way to advance our knowledge is finding inconsistencies in existing explanations (Garfinkel, 1983; Harman, 1965).

In order to be able to categorise the complexity of nature we need to be able to recognise reoccurring patterns as well as differences and similarities in the phenomena we encounter. A forest-living primate for example, which is able to detect a stalking predator in the undergrowth can flee from it before it is attacked and by surviving increases its chance to transmit its genes. Pattern recognition is therefore essential for survival, possibly in the entire animal kingdom (Edelman, 1987). Our human ability to make predictions is based on this ability to recognise patterns.

Explaining a natural phenomenon makes it necessary, due to the complexity of the environment, to view it separately from the entirety of its surrounding influences. It makes it also necessary to extract only its important dependencies. This especially applies to behavioural research. The problem of this approach is that the further we unhinge a phenomenon from its environment, the higher the probability of missing important factors influencing it and therefore missing

the goal of understanding the phenomenon all together. This illustrates the trade off between the process of categorisation and systematic observation of a phenomenon (Gould and Lewontin, 1994). In order to categorise we need to separate the phenomenon from its surrounding variables. This is done for example in psychology in laboratory experiments in which sets of interacting variables are systematically tested. Especially in social science this can also be done with agent based models, because they allow an even more controlled environment than laboratory experiments (Hoelzer and Melnik, 2005). It is essential to understand how good experiments are designed, because this process is very similar to the process of testing a computer aided model. Categorisation is the first step in this process and also the first step in finding an explanation.

In summary categorisation is the recognition of regularities, which by our assumptions describe the essential nature of an observed phenomenon.

### **10.1.3 Different philosophical approaches to define explanation**

The explanation of a phenomenon is the goal of every scientific endeavour and therefore also of agent based models used in the scientific process. According to Hempel (1965) an explanation is an expression of the need to gain predictive control over our future experiences. Its explanatory value is to be measured in terms of its capacity to produce this result. This definition requires that an explanation makes use of at least one law-like generalisation. But it is not possible to prove the universality of such an explanation (Hume, 1748). For example the fact that an object on earth falls to the ground a million times doesn't mean we know for sure that it would do this every time we let it fall. Universal statements are never completely verifiable, they are only falsifiable. Only existential statements are verifiable.

Popper (1934) gives a prototypical example of a non-verifiable universal statement as well as the rephrased existential version of the same statement which is verifiable. The universal statement is "All swans are white!" The existential version is "There are non-white swans!" Since the goal of the scientific process is to find answers or at least the model which fits the observed data best, a good

scientific explanation needs to be falsifiable. For computer based models used in science the same criterion applies. If a computer based model can explain anything or is not well theoretically grounded its explanatory value is very low. Additionally for computer based models it is important to thoroughly document how each of its variables is implemented to enable other researches to replicate and criticise its dynamics.

Since explanations include abstractions of real phenomena and since they are with raising levels of abstraction more and more generalizable, their advantage is that their explanatory value raises with their level of abstraction. The disadvantage is that the more abstract a concept is, the harder it is to observe. As a result it is very important to choose the right categories to base our abstraction on in order to generate a valid and generalisable explanation (Smith and Osherson, 1984), because it is this generalizability that enables us make predictions.

In general the explanatory value of an idea can be described as the result of two different processes. The first process is its empirical verification and the second process is its theoretical foundation. Incoherence in the theoretical foundation of a theory leads to incoherence in the theory in general, because the theoretical foundation is a precondition for any observation. As mentioned above in order to recognise something we always need an idea of what and how this something could be recognised (Thagard, 1978; Lipton, 1991).

Experiments deal in general with the empirical verification of an explanation and are used extensively in scientific research. The second process is often subject to less attention. Bridging the gap between empirical verification and theoretical foundation of an idea is the role of modelling and therefore also of ABM in science! In order to describe this function in more detail a definition of what a scientific theory is will be given.

## 10.2 Theories

One possible definition of a theory is a system of propositions with an explanatory value. A proposition with explanatory value is called a hypothesis (Thagard, 1989) and is a generalisation of experiences and a prediction of consequences.

The criteria for the explanatory value of a theory are equivalent to the criteria for the quality of a theory. Modelling, especially ABM, is a method to test these criteria, like experiments are a method to test the empirical validity of a theory.

A model is a system of theories (Zeigler, 1976). It is a sophisticated form of relating different assumed causal relations with each other. The way models should be built and how they should be related to empirical evidence has been one of the central questions in philosophy and science over the past centuries. The underlying question of this problem is, what do we take as evidence for the way we assume our reality is structured? (Rykiel, 1996)

Epistemology provides a set of rules to differentiate scientific theories from folk theories. A scientific theory should follow the rules of logic, it should be consistent and it should be sufficient. It should not contain any tautologies, its explanatory value should be as high as possible and it should be phrased in such a way that it is possible to test it with repetitive experimentation and empirical validation (Loehle, 1987). Scientific theories should be composed of testable propositions which are not yet empirically decided. As mentioned above these propositions are called hypotheses. Hypotheses are dynamic and can in this process be modified or even abandoned (Bortz and Döring, 1995).

The criteria for the quality of scientific theories are:

- consistency
- validity
- parsimony

In order to understand how ABM can help us to test these quality criteria of scientific theories, they will be discussed in detail in the next sections.

### **10.2.1 Consistency**

If a complex system of different theories is used to describe a phenomenon it is called a model. Models are normally used until they do not sufficiently explain



the empirical data any more. If the inconsistencies between the model and the observed facts become too severe one or more of the theories the model contains are modified or we create a new model altogether. As it is possible to test a theory by testing its hypotheses separately in experiments or systematic observations, it is possible to test a model by separately testing the theories it contains.

Every model is a simplification of reality, since humans always have a certain perspective from which they look at reality. This perspective determines what aspects of reality we assume to be essential for the solution of a given problem. In order to make any useful prediction it is necessary for hypotheses deriving from these aspects not to contradict each other. If a theory contains hypotheses which do not contradict each other it is called logically consistent. Logical consistency is one essential criterion for the quality of a scientific theory. It is at least as important as its empirical evidence. If a theory is not consistent it is not valid (Murphy and Medin, 1985; Bortz and Döring, 1995).

It is possible that hypotheses built into a theory are wrong but that the theory itself is consistent. In such a case it is very difficult to detect the mistake especially if it contains a high number of hypotheses. This is one of the great dangers in modern science and the reason for a very careful use and throughout testing of theories in research. ABM is one of the tools which can be used to test the consistency of scientific theories. The process of modelling makes the modeller pay attention to every aspect of the theory in order to enable a working implementation. If it contains inaccuracies, they will become evident.

### 10.2.2 Validity

The validity of a theory is strongly related with its empirical evidence. Validity can be defined as the degree to which the empirical data matches the prediction of the theory trying to explain the phenomenon in question. The more the explanatory content of a theory is represented by empirical data, the higher is the validity of this theory.

There are different types of validity. Each type addresses a specific methodological question and all four different types are built on one another. The basic type of validity is called *conclusion validity*. It answers the question: “Is there a

relationship between the theoretically assumed cause and its effect?” The *internal validity* is based on the *conclusion validity* and addresses the question: “Assuming that there is a relationship between the effect and its hypothetical cause, is this relationship a causal one?” (Steinke, 2000).

The relationship between two variables can be caused a factor, which is influencing both variables. A famous example is the observed positive correlation of the number of storks and the birth rate in Germany since the end of the 19th century (Hoefer et al., 2004). One possible conclusion is that storks deliver human babies, because the decrease in numbers of storks in central Europe was followed by periods of decreasing human birth rates. This explanation has of course no *internal validity*, because there is no evidence for the empirically observed relationship to be causal. It is more plausible to explain this correlation as a result of the industrialisation of Europe during the observed time period. Due to the pollution of the environment and due to increased urbanisation the number of storks was reduced, while the increasing economical productiveness and wealth has resulted in lower birth rates, ignoring the influence of the two wars during this time period (Matthews, 2000).

A third type of validity is *construct validity*. It answers the question: “Assuming that the relationship between the effect and its theoretically assumed cause is causal, how well does the empirical research reflect the theoretical construct and how well does the method of measurement reflect the construct of the measure?”.

In mammals for example there is a correlation between brain mass in relation to body mass and cognitive capacity. But is it justified to measure the brain to body mass ratio of humans to test their intelligence? The question is here, whether the brain to body mass ratio has conceptually the same empirical content as the construct of intelligence. *Construct validity* is given, if the construct to be measured and the method of measuring is equivalent.

The fourth type of validity is called *external validity* and refers to the problem of generalisation. It asks the question: “Assuming that there is a causal relationship between the constructs of the cause and the effect, is it possible to generalise this relationship to other situations?”

All four types of validity deal with the relationship between a theoretical construct

and empirical data and all four types have to be answered positively in order to make a meaningful prediction. Agent based models themselves can never be validated in such a way that it can be said they are true or not, but only that they are logically consistent. Like any other model they only show how the phenomena they try to explain would function if the theory they are based on is true (Klüver, 1998). This illustrates the bridging function of ABM between empirical research and theory construction (Rykiel, 1996).

### 10.2.3 Parsimony

The principle of parsimony is also called *Occam's razor* after the medieval English logician William of Ockham. He proposed that an explanation should not be more complicated than necessary. This principle is generally translated into two rules for theory construction:

1. If there is more than one possible theory explaining the same phenomenon, the simplest explanation should be favoured.
2. The structure of the relations between the hypotheses of a theory should be built as simply as possible.

An example for how useful, but also how misleading the principle of parsimony can be is the discovery of the planet Neptune. The calculations and the actual movement of the planet Uranus, done by Bouvard in 1821, showed discrepancies. This led Bouvard to hypothesise the existence of an eighth planet to be responsible for these irregularities. But the idea to assume an additional planet is only one possibility to explain the observed irregularities. The theoretical foundation of Bouvard's calculation were Newton's gravitational laws. Bouvard could have also assumed Newton's laws to be wrong. Only the criterion of parsimony led him to favour the "simpler" explanation, because rejecting Newton's gravitational laws would have questioned the entire theory of celestial mechanics. Based on Bouvard's theory the planet was found in 1846 by Galle. In this case using the principle of parsimony led to the right conclusions (Baum and Sheehan, 1997).

In 1843 LeVerrier found similar discrepancies in the orbit of Mercury around the Sun. Like Bouvard he followed the principle of parsimony and assumed the

presence of a small planet inside the orbit of Mercury to be the reason for the discrepancies instead of questioning Newton's gravitational laws. He proposed the name "Vulcan" for the Planet. But "Vulcan" was never found. In this case the more complex explanation was right: Newton's theory is only explaining gravity in the special case of relatively small gravitational fields. But Einstein's theory of relativity explained the perturbations of Mercury as a by-product of the Sun's gravitational field (Ni, 2005).

Parsimony is therefore a criterion for the practicability of an explanation beyond its empirical evidence, but empirical evidence is the more important of both criteria. Parsimony is also a criterion for the practicability of agent based models. The process of operationalisation of variables in order to implement them in an agent based model forces the modeller to find parsimonious solutions for complex problems because like theories, with increasing complexity their results become harder to interpret (May, 1976).

### 10.3 The task of modelling in science

The empirical content of a model can never be bigger than the empirical content of the theory it is supposed to simulate. Theories represent reality in such a way, that reality is reduced to basic principles. Therefore theories are already simplifications towards the essential (Morgan and Morrison, 1999). This confinement to the essential — to a few basic principles — is what makes a theory different from a description (Hanson, 1959).

The approach to understand the complexity of nature by a few basic principles is called reductionism. To understand the necessity of the reductionistic framework of science is fundamentally important for the understanding of the function of modelling in science (Gilbert, 1995). From the reductionistic position each *complex* system is nothing but the sum of its parts and can be reduced to accounts of individual constituents. As discussed above the selection of a phenomenon in order to explain it already includes an implicit theory about the nature of this phenomenon. Building an agent based model means to make the implicit assumptions a theory is based on explicit.

A model is neither a description nor a theory. It is the reconstruction of a theory. Hence a model is not directly verifiable (Premack and Woodruff, 1993). As mentioned in section 10.2.2 it is not possible to validate a theory in such a way that it can be said it is true or not, but only that it is logically consistent. The problem is that the inconsistencies of a theory become visible generally by comparing the empirical findings with the different predictions of the theory. The necessity to test the logical consistency of a theory is linked to the main problem of the reductionistic approach: explaining complexity (Axtell and Epstein, 1994; Nowak and Latane, 1994).

The complexity of a theory is created by the number of variables its hypotheses contain. All falsifiable hypotheses contain at least one dependent and one independent variable. If a theory contains only one hypothesis the predictions would be a one-to-one result of the assumed mathematical combination between the two variables of the hypothesis. The only problem with such a theory would be the comparison of its predictions with the empirical data. In modelling this process is called “model fitting” (Pimm, 1984).

But with more than one independent variable in relation to the prediction of the effect on one dependent variable the problem of interaction effects arises. Two independent variables interact if a particular combination of these variables leads to results that could not have been anticipated on the basis of the isolated main effects of these variables (Busemeyer and Jones, 1983). For example the effect of smoking on the probability of getting cancer is bigger for people who drink than for people who do not drink. The interaction effect becomes visible in the combination of the effects of both variables. In this case the effect of smoking differs depending on whether drinkers or non-drinkers are being tested.

An interaction does not necessarily imply that the direction of the effect is the same for different levels of a variable (Aiken and West, 1991). In medicine adverse effects may be caused by the interaction of different drugs which interact agonistically or antagonistically. As result different drugs could increase or annihilate their intended therapeutic effect.

The last two examples describe two-way interactions because they involve two independent variables. It is possible to describe the different results of such interactions, but the interpretation of these results becomes increasingly difficult.

The results of a model with a three-way interaction (three different independent variables involved) are even harder to interpret. A three-way interaction occurs whenever the results of a two-way interaction differ depending on the level of a third independent variable. This higher order interaction does not directly describe the relation between the main effects of each independent variable, but it describes interactions between other interactions.

This is the starting point of computer based modelling in science in general and specifically ABM in social science. Since any theory contains at least two hypotheses and these hypotheses create in most cases interaction effects, it is advisable to first simulate the theory before comparing it with empirical data. Because such a comparison makes only sense if we understand the predictions of the theory. In social science theories usually deal with the interactions of individuals. Since ABM enables the researcher to implement individual agents, it is an appropriate tool to test the interaction effects between hypotheses about the interactions of individuals.

### **10.3.1 Summary**

Sections 10.1 and 10.2 gave an overview of the process of theory building and about the criteria of what a good theory is. They also described the different roles ABM can play in the scientific process. The general function of ABM in the science is to bridge the gap between empirical verification and theoretical foundation of an idea. More specifically ABM can help to test the consistency of a theory, because the process of modelling makes the modeller pay attention to every aspect of the theory, which will make possible inaccuracies obvious.

Section 10.3 illustrated the necessity and the principles of a reductionistic view of science. From this point of view explanation means the description of a huge number of phenomena by a few basic principles. Emergent phenomena of high order interaction effects between variables such as weather or social structures pose limits to reductionism, but nevertheless they can be described within the classic reductionistic framework of science. In order to do so we need instruments which enable us to show how emergent phenomena are generated. Agent based models provide the means for the testing of such phenomena especially in social science. They enable researchers to examine effects generated by the interactions

of agents with different individual characteristics in the same environment. This ability to model individual agents and their adaptability to different research questions makes agent based models especially useful in behavioural research.

## 10.4 ABM in the case of this dissertation

The specific property which makes ABM especially useful for the operationalisation of social behaviour in primates is that it assumes individual based behaviour. In comparison with equation based models, in which every agent has the same attributes at any given point in time, agent based models enable the simulation of agents with different individual attributes and states. These agents can perform different action patterns depending on these individual states. This is the reason why the method of agent based modelling comes closer to a more ecologically valid simulation of social behaviour.

Even though compared to equation based models agent based models enable a more realistic simulation of inter-individual behaviour, they are not necessarily a more realistic representation of a theory. During the process of modelling the question has always to be kept in mind: “What is the key component of the theory and what is the best way to implement it into the model?” The more profound the basic ideas of a theory are operationalised, the better represented by a model will this theory be.

One of the best known agent based models in the field of primatology is Hemelrijk’s DomWorld. The process of replicating her model and examining it in detail lead to the conclusion that some details of DomWorld are insufficiently operationalised (see chapter 5). The fact that DomWorld is not explicitly claiming to model one of the basic theories dealing with the evolution of social behaviour, but examining higher levels of social organisation like male-female dominance behaviour, can be seen as disadvantage, because the absence of an explicit point of theoretical reference makes an exact operationalisation of the development of the differences in social structures in primate societies almost impossible. A model needs to refer to an explicit theoretical and empirical background in order to be falsifiable and like for any other good scientific theory this needs to be one the criteria of a scientific model. From this perspective this dissertation represents

the first systematic attempt of a consequent operationalisation of theories based on behavioural observations in order to explain the reasons for different forms of social structures in gregarious animals.

Another substantial contribution, besides the replication of Hemelrijk's model and its discussion, is the application of the ABM approach in the context of other explanatory theories of the development of social behaviour in primates and the testing of the coherence of the PIT and the SET, as discussed earlier in this chapter.

Beginning with the basic principles of group formation based on Hamilton's theory and adding generations and a dominance transmission function into the model showed that a change in dominance structure cannot only be achieved by random variation in the characteristic of a trait promoting dominance, but that it also needs environmental conditions which select for this characteristic. In the case of the *dominance inheritance model* this environmental condition was the predation pressure. In this model each agent had the same dominance value in the beginning of the simulation +/- a small random variation. Without predation in the environment the average dominance value was stable, with predation it increased. Since the dominance value was a measure for the ability to displace other individuals, the model showed that by adding predation to an environment, the agents with a good ability to displace other individuals were more successful in having offspring and transmitting this displacement ability or dominance. This could be one possible explanation how social dominance evolved. The PIT focuses mainly on genetic random variation to explain the differences in the social structure of different primate species, yet adaptation is always related to the environment the individuals live in. Explaining fundamental differences between species like their social structure only with genetic drift and leaving out environmental pressures seems to be insufficient from the perspective of the results of the *dominance inheritance model* and also from the perspective of the empirical findings.

If we assume that environmental factors like predation and food availability and distribution have certain effects on the evolution of social structure and then compare our assumptions with the empirical findings from primate research the explanatory approach of the SET provides a good fit for most of the data. During the process of modelling the SET the key component separating the despotic and



the egalitarian agents in the PIT and the SET became clear. In both theories it is the spatial distance between the agents in a group. The function of this distance seemed to be different in the two theories. In the PIT despotic species are characterised by wider distances between individuals. Following his concept the distances are wider because subdominant individuals try to avoid confrontations with dominant individuals. In the SET despotic social structures have evolved as a result of increased predation pressure which forces the individuals of a group closer together on average. From this perspective predation would be the cause and the form of social organisation would be the effect.

The critical point seems to be that in both theories spatial distribution is operationalised differently. This becomes obvious in the process of modelling because it makes one pay more attention to the details of the theory. A theory has to be complete enough to be simulated on a computer. If it contains inaccuracies, than they will become evident during their implementation.

The PIT defines spatial distribution as distance between individuals, like a personal space relative to the size and circumference of the group territory. The SET describes it as group density. The understanding that both theories operationalise the same term possibly only with a different content could lead to a better understanding of the empirical connections in the description of primate societies. A comparison of both explanatory approaches should emphasise more on their commonalities than their differences. From this perspective such a theoretical synthesis would be the best solution and point to a more holistic theory. Both the phylogenetic history of a species as well as the environmental conditions it lives in shape the evolution of its social structure. Social behaviour is like any other characteristic of a group of individuals the result of environment and genetics.

The third agent based model of the thesis also emphasises this point. It especially shows the usefulness of ABM in behavioural science by illustrating the flexible structure mentioned above. The existing dominance inheritance model is modified and extended in order to test a variety of theories. Showing the adaptiveness and role of social dominance and the effect of female mate choice and male variance is as interesting as showing the effect dominance interactions between equally dominant individuals have on group dominance and fitness.

Another important point of this work is the understanding of the necessity of a easy to use programming environment which enables the researcher to visualise both the interactions and movements of the agents and the results. Especially the visualisation of the agents was very important for this work and made the modelling process much more intuitive. Being able to visualise the behaviour each single agent and an easy to learn programming language makes NetLogo very suited for the task. Even researchers who have very limited experience with programming can easily construct and program their own models with this environment because of an extensive online documentation and large library of available models on different topics.

## 10.5 Summary

ABM is a very useful tool in order to test the consistency of existing theories and to find new explanatory approaches to natural phenomena. It is important to be aware of the restrictions of the ecological validity the results of the models have. They can serve as aid in finding problems by modelling different possible variables causing a certain effect. The best way of doing so is, as demonstrated in this work, to start with a simple model of a well known and established theory and then add step by step new factors which are the subject of related or different theories and test their effects one by one.

During the progress of this thesis it became clear that starting with an existing model on a similar topic is the best way to understand the dynamics of an agent based model. The biggest advantage of ABM compared to population modelling is the ability to model individual-level variation in traits and behaviour. The difference to population models is their focus on the single individual. Especially for species with higher cognitive functions like primates, hyenas or dolphins this approach can be very useful in order to understand their social group dynamics.



# Chapter 11

## Conclusion

This work had two objectives. One was the successful implementation of agent based models in the field of social ecology, the other was testing the coherence of different theories from this field. The use of agent based models in behavioural science is still controversial. While well represented in economics, their explanatory value in behavioural research has been questioned (O’Sullivan and Haklay, 2000; Epstein, 1999). The dissertation helps to broaden their use by giving examples of how to agent based models to examine different theories from about the evolution of social dominance and social structure.

A large set of observational data on different species of primates has been accumulated over the past decades. Differences and similarities in the interaction patterns of different species have been found. This has led to a variety of different theories to explain these differences. With the agent based models in this thesis it was possible to test the coherence of some of these theories. In the case of the socio-ecological theory and the phylogenetic inertia theory this led to a clarification of the differences of the two theories concerning the assumed different spatial distribution described by both. In the case of Hemelrijk’s theory it made problems with the operationalisation of some of the factors the theory is based on visible.

## 11.1 Contributions

Before this work was started DomWorld was the only well established agent based model in primatology. It was successfully replicated in this dissertation and critical points in the implementation of different variables were found, discussed and suggestions about possible improvements were made. The code of the replication is available online for public discussion and has already spawned various critical comments and further replications.

The first new model of this thesis was an implementation of Hamilton's theory about the initial reasons for the evolution of social dominance and gregariousness. It was based on spatial distribution and hereditary transmission of social dominance and its results match the predictions derived from the theory it is based on. The model can be seen as successful implementation. The results show, as predicted by the theory, that social dominance, if represented as ability to displace conspecifics, is adaptive because it enables individuals to avoid predation by maintaining a central position in the group (Sapolsky, 2005).

The second new model of this dissertation tested the effects of predation, food availability and food distribution on two populations with different social structures. The differences in the social structure were operationalised via different spatial characteristics based on the descriptions given by the socio-ecological theory. The model tested the coherency of the socio-ecological theory by comparing the results of the performance of the two populations in different modelled environmental conditions with the predictions of the theory. The results of the model fit these predictions and findings from empirical research, implying that the socio-ecological theory is consistent and that the implementation was successful. In comparing the phylogenetic inertia theory and the socio-ecological theory it became visible that both deal with the same phenomena but use different definitions for spatial distribution. The phylogenetic inertia theory and the socio-ecological theory are seen as opposing theories, but in providing an explanation for the primary discrepancy between them, they have been unified in this dissertation.

The last set of models presented are an extension of the dominance inheritance model and test the effects female mate choice, male variation and rank fights have on the evolution of social dominance. The results of these extensions match

different observations and predictions about the interaction of the tested selective factors with social dominance. The way these factors were implemented in the model was chosen to demonstrate that by maintaining the general structure of an agent based model and adding one variable after another to it, it is possible to test a variety of different theories on a similar topic.

All of the models in this dissertation provide a platform for further research and discussion in the field of behavioural ecology and for the implementation of further developed and extended agent based models. They should be seen as encouragement for critical discussion of existing theories and of the methodology itself.

As mentioned in the beginning of this chapter the use of agent based models is discussed controversially in social science. The main reasons for this are a misunderstanding of what an agent based model can and cannot do and a lack of transparency in the implementation process of already existing models. The epistemological discussion of the functions models have in science in general and agent based models in particular at the end of the dissertation aimed at clarifying some of the misconceptions. Its main statement is that agent based models are theory building tools. They can never be a substitute for empirical research, but they can help to test the consistency of existing theories and based on these tests can help to make suggestions for possible modifications. These in turn would have to be tested with empirical research.

Starting with an existing model on a similar topic proved to be the best way to understand the dynamics of an agent based model. The biggest advantage of ABM is its ability to model individual level variation in traits and behaviour. Especially for species with sophisticated social structures this approach can be very useful in order to understand their social group dynamics.

NetLogo was chosen as development environment for the implementation of the models. Its intuitive structure and the possibility to easily visualise agent movements and results proved to be very useful for the work in this dissertation. It can be recommended for further use in the field of behavioural research.

The effort to improve ABM as technology and make it easier to use for researchers in different fields dealing with social phenomena is another contribution of

this dissertation. It was done by systematically describing the process of development and implementation of different models, by providing information about the environment used and also by publicly providing the developed code.

## 11.2 Future Work

Existing agent based models in social science tend to be developed in isolation with individual behaviours being programmed for the specific simulation in mind using a variety of (largely incompatible) simulation toolkits. This lack of interoperability and re-use leads to the need for researchers to replicate existing models in order to investigate new ones, at the cost of time and effort. A possible solution to this problem would be the development of an online “library” of agent based models, each dealing with a different aspect of social behaviour. Such a library could be used as a database for researchers of different fields and also enable students to explore the dynamics of the theories they are studying in an intuitive way. The models in such a library could serve as “construction kit” for new models and different theories. The advantage would be, that researchers could test the consistency and plausibility of their theories before going into the field. In order to create such a library a common (computational) language and standardised specification for the interpretation and analysis of such models would be required. This dissertation represents a step in this direction.

ABM can be helpful to test theories about the evolution of the social systems in most animal species with a sophisticated social structure. Research on spotted hyenas has shown that they have a highly developed matrilineal social structure (van Horn et al., 2004; Glickman et al., 1997), which makes them a good subject for ABM. In addition, a large body of observational data about social interactions in different bird species has been collected and there is an increasing interest for this data to be modelled. By modelling the evolution of social systems in species from different taxa, underlying general mechanisms could become visible and help to understand the evolution social structure in more general terms.

In order to make ABM more attractive to researchers from different fields, it is necessary to simplify the implementation process. NetLogo as tool is well suited for this task, but still requires a considerable amount of programming. The

reduction of the programming effort could reduce the reluctance to use ABM in behavioural field research. The construction of a development environment in which researchers could choose and combine pre-programmed behaviours from a behaviour library, like the one mentioned above, to test their interaction effects would be a step in a more user friendly direction of implementing ABM.

In primatology more empirical data with focus on the spatial distribution of individuals in different macaque species should be collected or the existing data should be re-examined from the perspective of spatial distribution in order to empirically test the theoretical explanation for the primary discrepancy between the socio-ecological theory and the phylogenetic inertia theory found in this dissertation. Also more data about the signals used by primate females to choose mating partner should be collected to test empirically the modelled effect female mate choice has on social dominance and quality.





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# Chapter 12

## Appendices

### 12.1 Appendix A

In this appendix are the results of the secondary dependent variables of the MSI-step2 presented. These variables are number of offspring, number of agents died on starvation and number of agents killed by predation. The results are ordered in such a way, that each section represents the condition it is labelled with, starting with the condition representing an environment with equally distributed food resources.

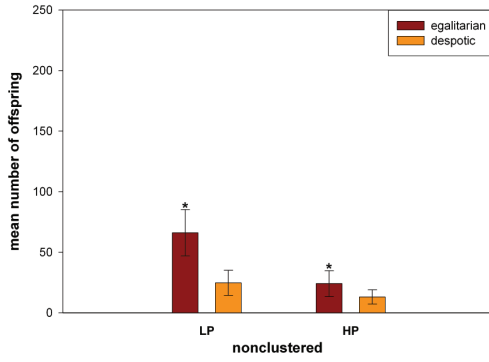
#### 12.1.1 Results for the three secondary dependent variables in the MSI-step2

##### Non-clustered condition

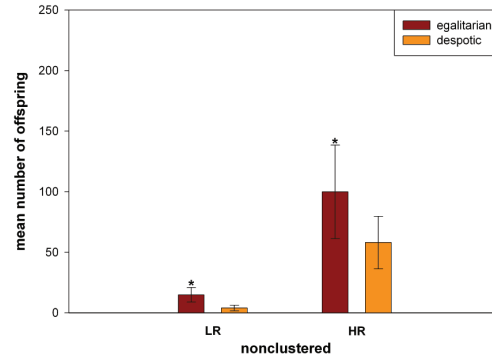
**Number of offspring:** With a stable regrowth-rate and equally distributed food resources the egalitarian agents produced more offspring in both of the conditions, with low and high predation-rate (LP [N = 100, t = 19.1, p < .001], HP [N = 100, t = 9.06, p < .001])(Figure 12.1a).

With a stable predation-rate and equally distributed food resources the egalit-

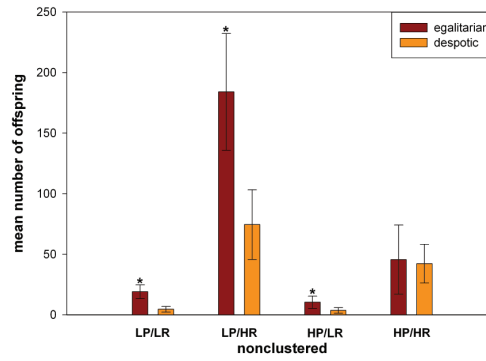




(a)



(b)



(c)

Figure 12.1: Average number of offspring for high and low predation rates (a), high and low regrowth rates (b) and for the interaction between the different predation and regrowth rates (c) in the *non-clustered* condition

arian agents produced more offspring in both of the conditions, with low and high regrowth-rate (LR [N = 100,  $t = 16.98$ ,  $p < .001$ ], HR [N = 100,  $t = 9.46$ ,  $p < .001$ ])(Figure 12.1b).

The egalitarian agents produced significantly more offspring in three of the four combination conditions with equally distributed food resources (LP/LR [N = 100,  $t = 23.86$ ,  $p < .001$ ], LP/HR [N = 100,  $t = 19.54$ ,  $p < .001$ ], HP/LR [N = 100,  $t = 12.1$ ,  $p < .001$ ]). There was no significant difference between the two groups in the condition with high predation-rate and high regrowth-rate [N = 100,  $t = 1.03$ ,  $p = .3$ ](Figure 12.1c).

**Number of agents starved:** With a stable regrowth-rate and equally distributed food resources significantly more despotic agents starved to death in both of the conditions, with low and high predation-rate (LP [ $N = 100$ ,  $t = 6.55$ ,  $p < .001$ ], HP [ $N = 100$ ,  $t = 4.22$ ,  $p < .001$ ])(Figure 12.2a).

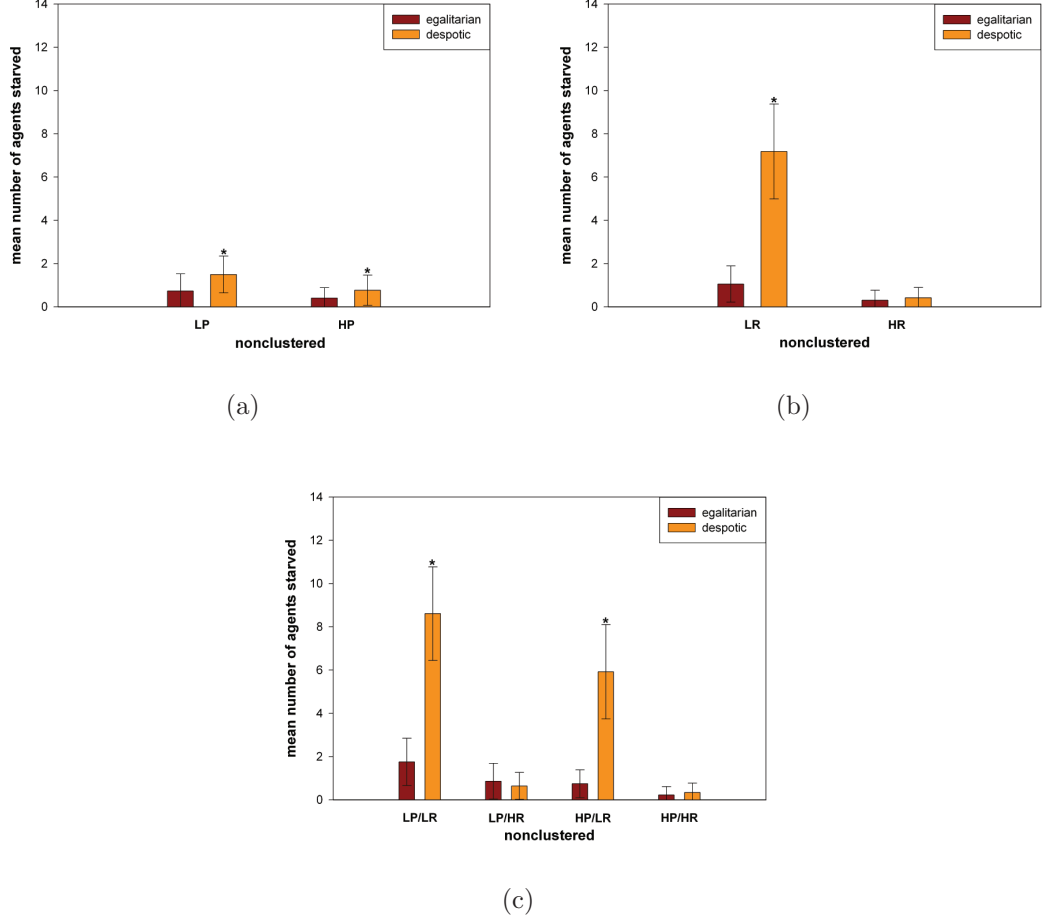


Figure 12.2: Average number starved agents for high and low predation rates (a), high and low regrowth rates (b) and for the interaction between the different predation and regrowth rates (c) in the *non-clustered* condition

With a stable predation-rate and equally distributed food resources significantly more despotic agents starved to death in the condition with low regrowth-rate (LR [ $N = 100$ ,  $t = 26.09$ ,  $p < .001$ ]). In the condition with a high regrowth-rate there was no significant difference between the two groups (HR [ $N = 100$ ,  $t = 1.68$ ,  $p = .0.09$ ])(Figure 12.2b).

With equally distributed resources significantly more despotic agents starved to death in the following conditions: LP/LR [ $N = 100$ ,  $t = 28.24$ ,  $p < .001$ ], HP/LR [ $N = 100$ ,  $t = 22.76$ ,  $p < .001$ ]. Significantly more egalitarian agents starved in

the condition with low predation and high regrowth-rate (LP/HR [N = 100, t = 2.13, p < .001]). There was no significant difference between the two groups in the condition with high predation-rate and high regrowth-rate (HP/HR [N = 100, t = 1.9, p = .06])(Figure 12.2c).

**Number of agents killed by predation:** With a stable regrowth-rate and equally distributed food resources significantly more egalitarian agents were killed due to predation in both of the conditions, with low and high predation-rate (LP [N = 100, t = 30.34, p < .001], HP [N = 100, t = 19.06, p < .001])(Figure 12.3a).

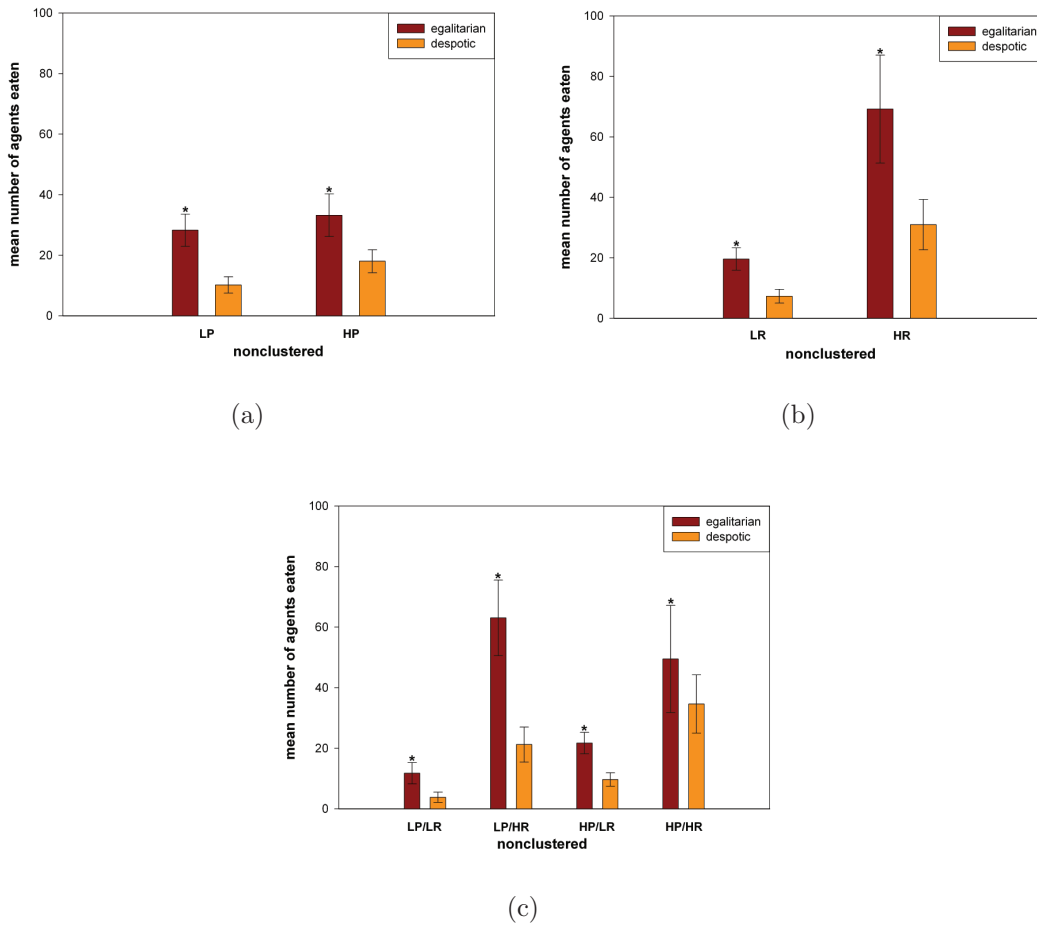


Figure 12.3: Average number of agents killed by predation for high and low predation rates (a), high and low regrowth rates (b) and for the interaction between the different predation and regrowth rates (c) in the *non-clustered* condition

With a stable predation-rate and equally distributed food resources significantly more egalitarian agents were killed due to predation also in both of the conditions, with low and high regrowth-rate (LR [N = 100, t = 28.28, p < .001], HR [N =

100,  $t = 19.42$ ,  $p < .001$ ](Figure 12.3b).

In all four different of the combination conditions with equally distributed food resources significantly more egalitarian agents were killed due to predation (LP/LR [N = 100,  $t = 20.22$ ,  $p < .001$ ], LP/HR [N = 100,  $t = 30.43$ ,  $p < .001$ ], HP/LR [N = 100,  $t = 28.81$ ,  $p < .001$ ], HP/HR [N = 100,  $t = 7.38$ ,  $p < .001$ ])(Figure 12.3c).

### Clustered condition

**Number of offspring:** With a stable regrowth-rate and clustered food resources the egalitarian agents produced significantly more offspring in the condition with low predation-rate (LP [N = 100,  $t = 10.81$ ,  $p < .001$ ]). There was no significant difference in the condition with high predation-rate (HP [N = 100,  $t = 1.09$ ,  $p = .28$ ])(Figure 12.4a).

With a stable predation-rate and clustered food resources the egalitarian produced significantly more offspring in both of the conditions, with low and high regrowth-rate (LR [N = 100,  $t = 11.17$ ,  $p < .001$ ], HR [N = 100,  $t = 3.66$ ,  $p < .001$ ])(Figure 12.4b).

The egalitarian agents produced significantly more offspring in three of the four combination conditions with clustered food resources (LP/LR [N = 100,  $t = 14.46$ ,  $p < .001$ ], LP/HR [N = 100,  $t = 6.18$ ,  $p < .001$ ], HP/LR [N = 100,  $t = 7.58$ ,  $p < .001$ ]). The despotic agents produced significantly more offspring in the condition with high predation-rate and high regrowth-rate (HP/HR [N = 100,  $t = .01$ ,  $p < .001$ ])(Figure 12.4c).

**Number of agents starved:** With a stable regrowth-rate and clustered food resources significantly more despotic agents starved to death in the condition with high predation-rate (HP [N = 100,  $t = 22.12$ ,  $p < .001$ ]). There was no significant difference in the condition with low predation-rate (LP [N = 100,  $t = 1.63$ ,  $p = .1$ ])(Figure 12.5a).

With a stable predation-rate and clustered food resources significantly more

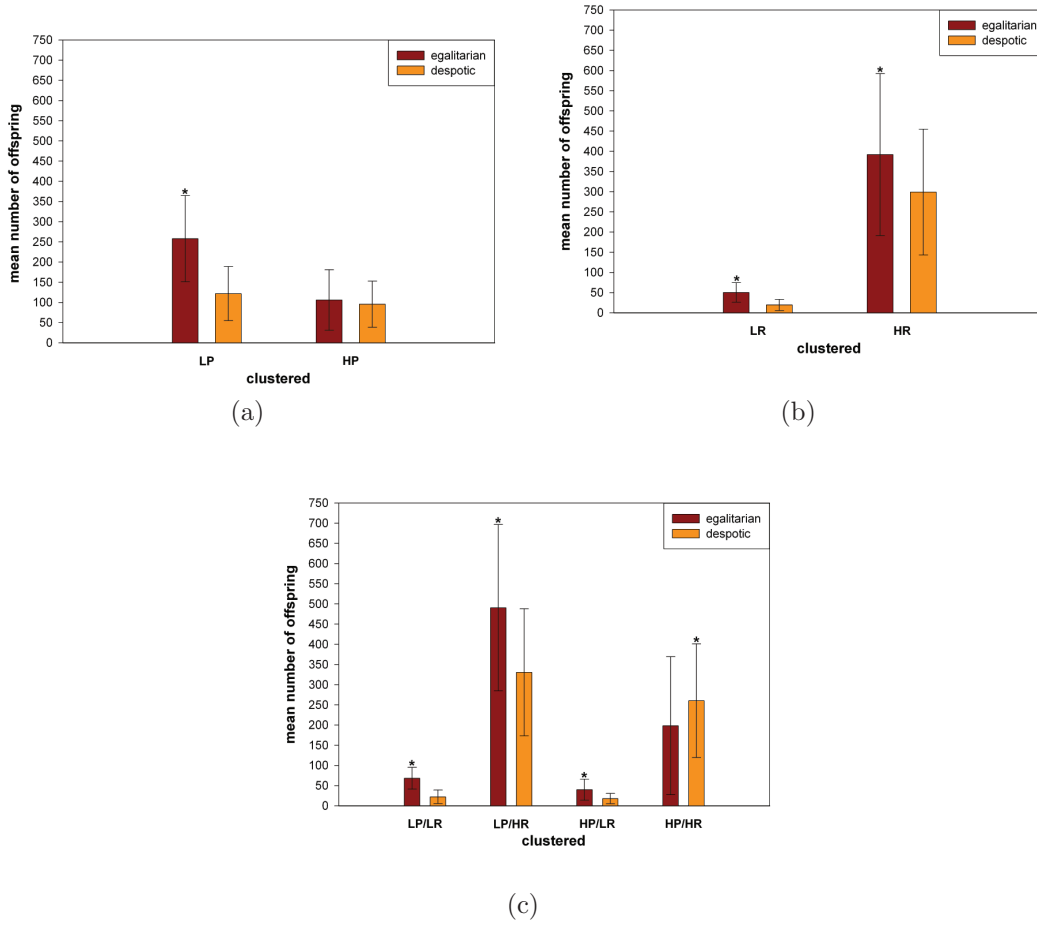


Figure 12.4: Average number of offspring for high and low predation rates (a), high and low regrowth rates (b) and for the interaction between the different predation and regrowth rates (c) in the *clustered* condition

despotic agents starved to death in both of the conditions, with low and high regrowth-rate (LR [N = 100,  $t = 13.75$ ,  $p < .001$ ], HR [N = 100,  $t = 13.17$ ,  $p < .001$ ])(Figure 12.5b).

Significantly more despotic agents starved in all four combination conditions with clustered food resources (LP/LR [N = 100,  $t = 2.3$ ,  $p < .02$ ], LP/HR [N = 100,  $t = 5.25$ ,  $p < .001$ ], HP/LR [N = 100,  $t = 19.53$ ,  $p < .001$ ], HP/HR condition [N = 100,  $t = 20.4$ ,  $p < .001$ ])(Figure 12.5c).

**Number of agents killed by predation:** With a stable regrowth-rate and clustered food resources significantly more egalitarian agents were killed due to predation in both of the conditions, with low and high predation-rate rate (LP

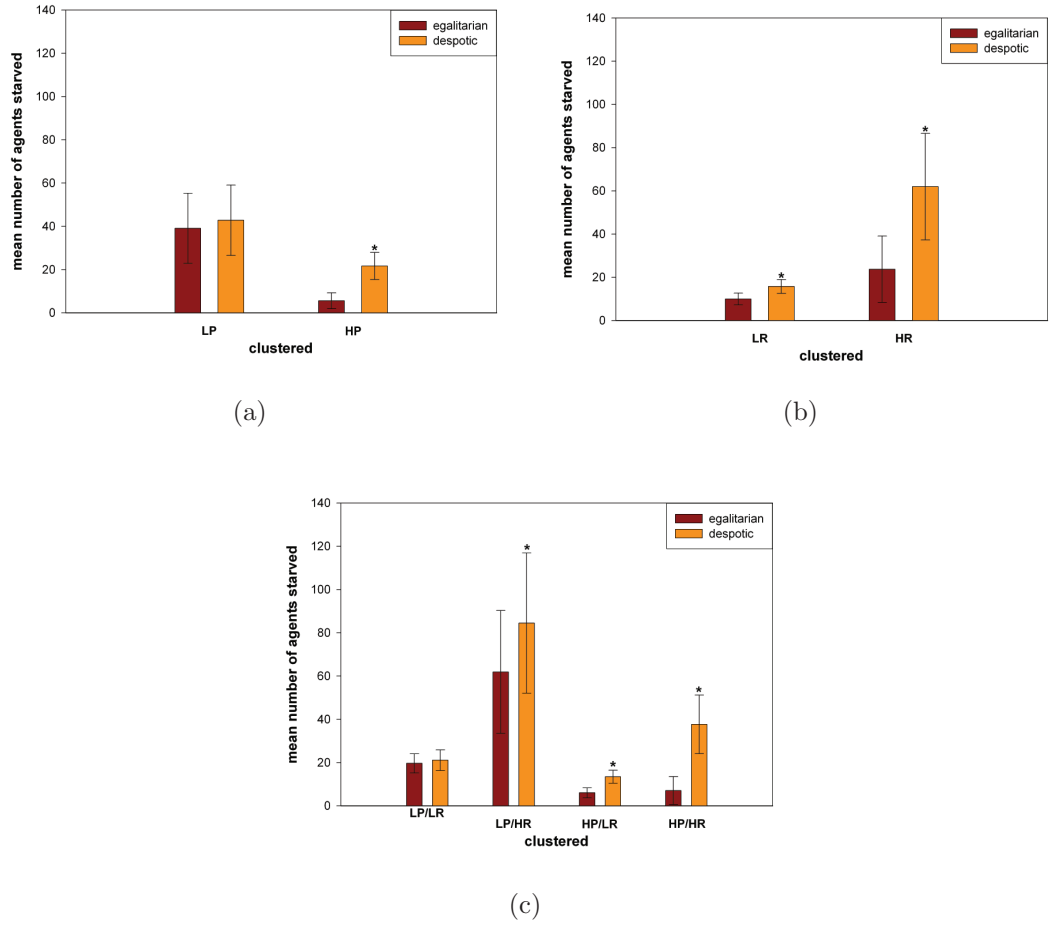
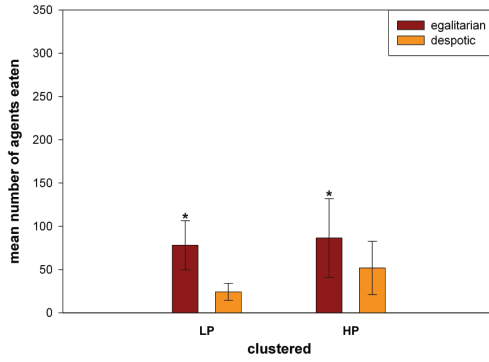


Figure 12.5: Average number of starved agents for high and low predation rates (a), high and low regrowth rates (b) and for the interaction between the different predation and regrowth rates (c) in the *clustered* condition

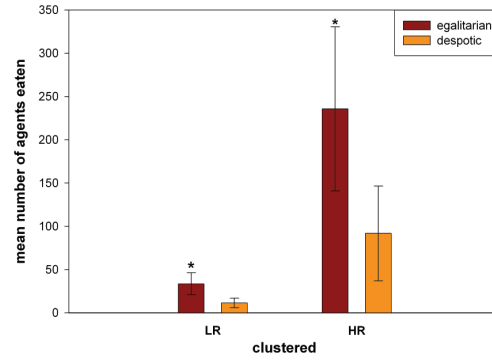
[ $N = 100$ ,  $t = 17.94$ ,  $p < .001$ ], HP [ $N = 100$ ,  $t = 6.3$ ,  $p < .001$ ])(see Figure 12.6a).

With a stable predation-rate and clustered food resources significantly again more egalitarian agents were killed due to predation in both of the conditions, with low and high regrowth-rate (LR [ $N = 100$ ,  $t = 15.85$ ,  $p < .001$ ], HR [ $N = 100$ ,  $t = 13.14$ ,  $p < .001$ ])(Figure 12.6b).

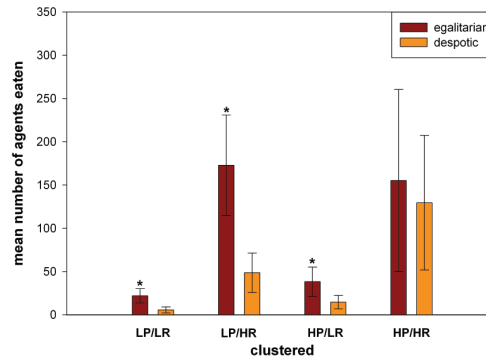
Significantly more egalitarian agents were killed due to predation in three of the four combination conditions with clustered food resources (LP/LR [ $N = 100$ ,  $t = 18.55$ ,  $p < .001$ ], LP/HR [ $N = 100$ ,  $t = 19.95$ ,  $p < .001$ ], HP/LR [ $N = 100$ ,  $t = 12.78$ ,  $p < .001$ ]). There was no significant difference in the condition with high predation-rate and high regrowth-rate (HP/HR [ $N = 100$ ,  $t = 1.96$ ,  $p < .001$ ]).



(a)



(b)



(c)

Figure 12.6: Average number of agents killed by predation for high and low predation rates (a), high and low regrowth rates (b) and for the interaction between the different predation and regrowth rates (c) in the *clustered* condition

.051])(Figure 12.6c).

### Comparison of the results of the clustered and the non-clustered condition for each agent population

**Number of offspring** The comparison of the different predation conditions shows, that the egalitarian agents produced significantly more offspring in settings with clustered food sources (LP [N = 100,  $t = 17.97$ ,  $p < .001$ ] and HP [N = 100,  $t = 10.79$ ,  $p < .001$ ]). The same is true for the despotic agents (LP [N = 100,  $t = 14.41$ ,  $p < .001$ ] and HP [N = 100,  $t = 13.92$ ,  $p < .001$ ])(Figure 12.7a).

The comparison of the different regrowth conditions shows, that the egalitarian

agents produced significantly more offspring in settings with clustered food sources (LR [N = 100, t = 14.33, p < .001] and HR [N = 100, t = 14.27, p < .001]). The same is true for the despotic agents (LR [N = 100, t = 10.99, p < .001] and HR [N = 100, t = 15.43, p < .001])(Figure 12.7b).

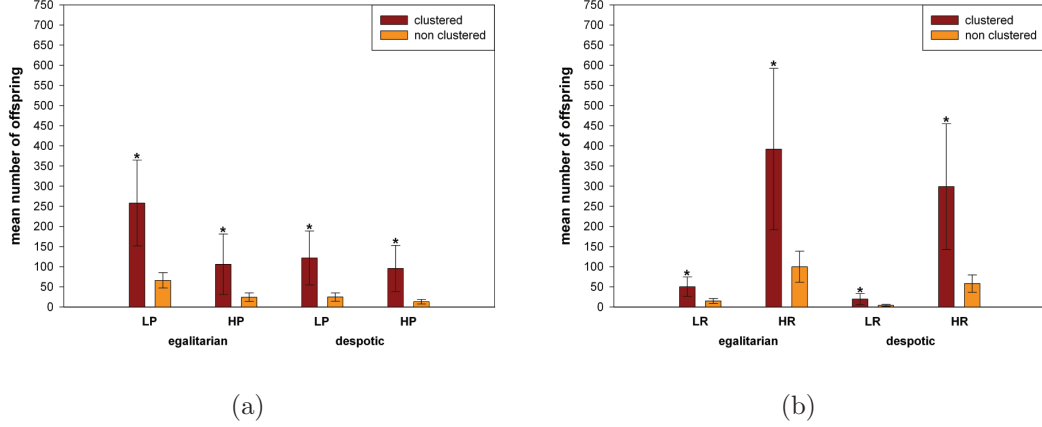


Figure 12.7: Comparison of the number of offspring in the clustered vs. non-clustered setting for the different predation conditions (a) and for the different regrowth conditions (b)

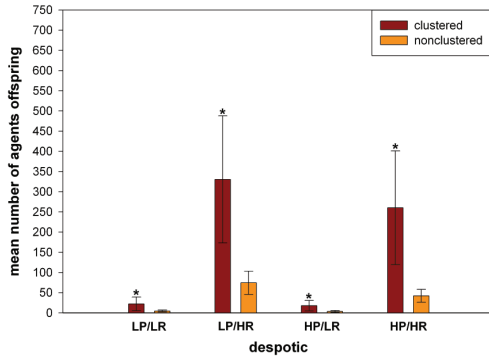
Compared with their performance in the nonclustered setting the egalitarian agents produced significantly more offspring in the clustered settings in all four conditions (LP/LR [N = 100, t = 18.44, p < .001], LP/HR [N = 100, t = 14.62, p < .001], HP/LR [N = 100, t = 10.85, p < .001] and HP/HR [N = 100, t = 8.75, p < .001])(Figure 12.8a).

Compared with their performance in the nonclustered setting the despotic agents produced also significantly more offspring in the clustered settings in all four conditions (LP/LR [N = 100, t = 10.44, p < .001], LP/HR [N = 100, t = 15.65, p < .001], HP/LR [N = 100, t = 11.03, p < .001] and HP/HR [N = 100, t = 15.69, p < .001])(see Figure 12.8b).

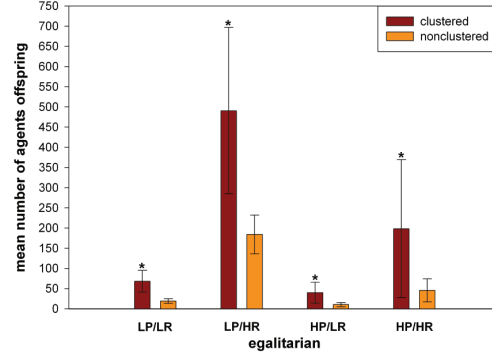
**Number of agents starved** The comparison of the different predation conditions shows, that significantly more egalitarian agents starved in settings with clustered food sources (LP [N = 100, t = 23.88, p < .001] and HP [N = 100, t = 13.64, p < .001]). The same is true for the despotic agents (LP [N = 100, t = 25.49, p < .001] and HP [N = 100, t = 33.08, p < .001])(Figure 12.9a).

The comparison of the different regrowth conditions shows, that significantly





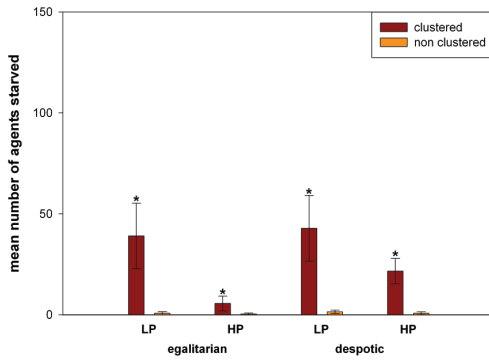
(a)



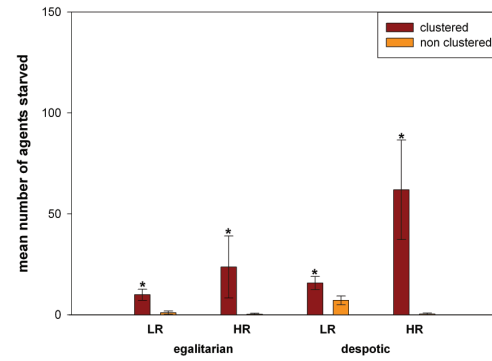
(b)

Figure 12.8: Comparison of the number of offspring in the clustered vs. non-clustered setting for despotic agents (a) and egalitarian agents (b)

more egalitarian agents starved in settings with clustered food sources (LR [ $N = 100$ ,  $t = 30.42$ ,  $p < .001$ ] and HR [ $N = 100$ ,  $t = 15.18$ ,  $p < .001$ ]). The same is true for the despotic agents (LR [ $N = 100$ ,  $t = 22.19$ ,  $p < .001$ ] and HR [ $N = 100$ ,  $t = 24.92$ ,  $p < .001$ ])(see Figure 12.9b).



(a)



(b)

Figure 12.9: Comparison of the number of agents starved in the clustered vs. non-clustered setting for the different predation conditions (a) and for the different regrowth conditions (b)

Compared with their performance in the nonclustered setting significantly more egalitarian agents starved in the clustered settings in all four conditions (LP/LR [ $N = 100$ ,  $t = 39.47$ ,  $p < .001$ ], LP/HR [ $N = 100$ ,  $t = 21.37$ ,  $p < .001$ ], HP/LR [ $N = 100$ ,  $t = 21.25$ ,  $p < .001$ ] and HP/HR [ $N = 100$ ,  $t = 10.44$ ,  $p < .001$ ])(Figure 12.10a).

Compared with their performance in the nonclustered setting significantly more despotic agents starved in the clustered settings in all four conditions (LP/LR [ $N = 100$ ,  $t = 24.47$ ,  $p < .001$ ], LP/HR [ $N = 100$ ,  $t = 25.76$ ,  $p < .001$ ], HP/LR [ $N = 100$ ,  $t = 21.17$ ,  $p < .001$ ] and HP/HR [ $N = 100$ ,  $t = 27.65$ ,  $p < .001$ ])(Figure 12.10b).

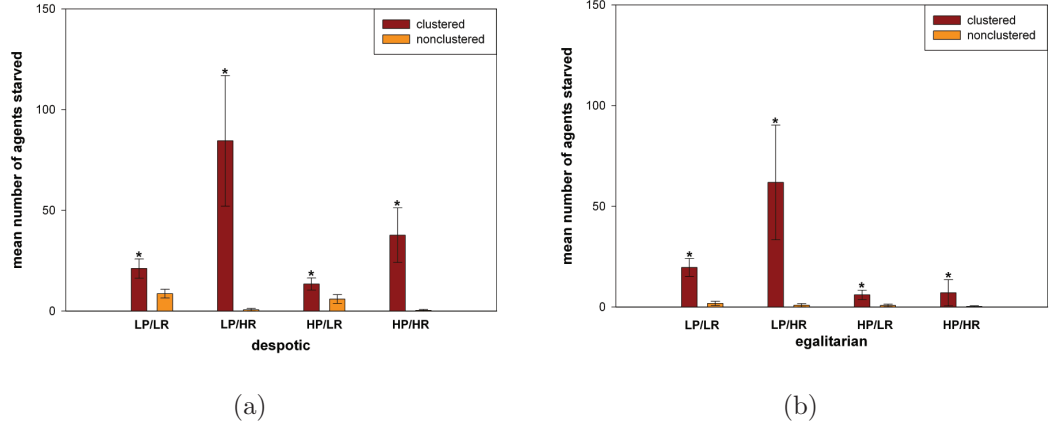
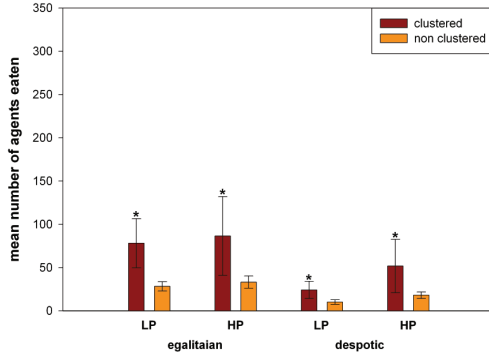


Figure 12.10: Comparison of the number of starved agents in the clustered vs. non-clustered setting for despotic agents (a) and egalitarian agents (b)

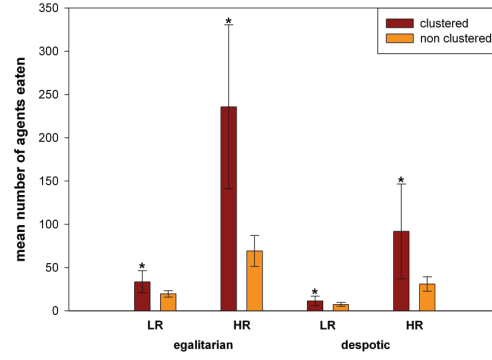
**Number of agents killed** The comparison of the different predation conditions shows, that significantly more egalitarian agents were killed by predation in settings with clustered food sources (LP [ $N = 100$ ,  $t = 17.36$ ,  $p < .001$ ] and HP [ $N = 100$ ,  $t = 11.6$ ,  $p < .001$ ]). The same is true for the despotic agents (LP [ $N = 100$ ,  $t = 13.75$ ,  $p < .001$ ] and HP [ $N = 100$ ,  $t = 10.54$ ,  $p < .001$ ])(see Figure 12.11a).

The comparison of the different regrowth conditions shows, that significantly more egalitarian agents were killed by predation in settings with clustered food sources (LR [ $N = 100$ ,  $t = 10.57$ ,  $p < .001$ ] and HR [ $N = 100$ ,  $t = 17.19$ ,  $p < .001$ ]). The same is true for the despotic agents (LR [ $N = 100$ ,  $t = 6.99$ ,  $p < .001$ ] and HR [ $N = 100$ ,  $t = 11.01$ ,  $p < .001$ ])(see Figure 12.11b).

Compared with their performance in the nonclustered setting significantly more egalitarian agents were killed by predation in the clustered settings in all four conditions (LP/LR [ $N = 100$ ,  $t = 12.13$ ,  $p < .001$ ], LP/HR [ $N = 100$ ,  $t = 18.73$ ,  $p < .001$ ], HP/LR [ $N = 100$ ,  $t = 9.73$ ,  $p < .001$ ] and HP/HR [ $N = 100$ ,  $t = 9.85$ ,  $p < .001$ ])(Figure 12.12a).



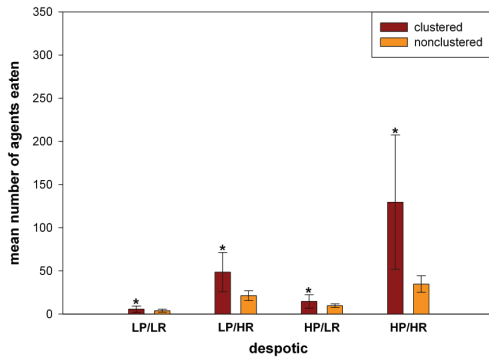
(a)



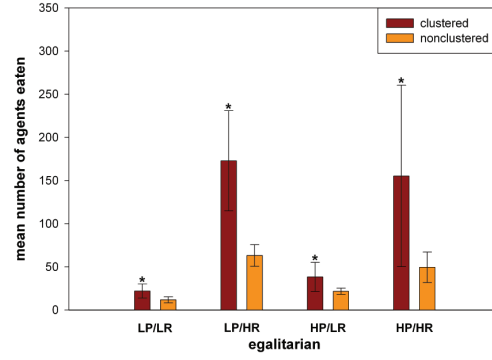
(b)

Figure 12.11: Comparison of the number of agents killed by predation in the clustered vs. non-clustered setting for the different predation conditions (a) and for the different regrowth conditions (b)

Compared with their performance in the nonclustered setting significantly more despotic agents were killed by predation in the clustered settings in all four conditions (LP/LR [ $N = 100$ ,  $t = 4.79$ ,  $p < .001$ ], LP/HR [ $N = 100$ ,  $t = 11.33$ ,  $p < .001$ ], HP/LR [ $N = 100$ ,  $t = 6.09$ ,  $p < .001$ ] and HP/HR [ $N = 100$ ,  $t = 12.43$ ,  $p < .001$ ])(Figure 12.12b).



(a)



(b)

Figure 12.12: Comparison of the number of agents killed by predation in the clustered vs. non-clustered setting for despotic agents (a) and egalitarian agents (b)

## 12.2 Appendix B

### 12.2.1 Model code

#### DomWorld Replication

```
;This research funded by The Engineering and Physical Sciences Research Council (EPSRC),
;Grant GR/S79299/01 (AIBACS),
;“The Impact of Durative Variable state on the Design and Control of Action Selection”.
;;;;;;;;;;;;; globale Variables ;;;;;;;;;;;;;;
globals(
PerSpace ;personal space
NearView ;close view
MaxView ;far view
time-units ;monitor to show the number of goes
male ;monitor to show the number of times of male interaction carried on
female ;monitor to show the number of times of female interaction carried on
aggmale ;aggressive interactions by males
aggfemale ;aggressive inteactions by females
vision-angle ;in what direction the turtle can see
search-angle ;where the turtle searches for other agents
min-dom ;minimal dominance value
randomrunnum
filename)
;;;;;;;;;;;;; breeds ;;;;;;;;;;;;;;
breed (males)
breed (females)
;;;;;;;;;;;;; monkey variables ;;;;;;;;;;;;;;
turtles-own (
attraction ;sexual attraction
StepDom ;intensity of aggression
dom-value ;hierarchy variablen
w ;win variable
diff ;the actual vision angle between two agents
opponent ;direkter Gegner
distanceP ;the distance zu Gegner
waitcount)
;;;;;;;;;;;;; setup-procedure ;;;;;;;;;;;;;;
to setup
ca
setup-globals
setup-patches
setup-turtles
end
;;;;;;;;;;;;; creates background ;;;;;;;;;;;;;;
to setup-patches
ask patches (set pcolor green) ;sets background green
end
to setup-globals
set PerSpace 2
set NearView 24
```

```

set MaxView 50
set vision-angle 120
set search-angle 90
set min-dom 0.1
set randomrunnum random 999999
end
;;;;;;;;;;;;; creates male and female monkeys ;;;;;;;;;;;;;;
to setup-turtles
create-males population
(set color black
set dom-value 16.0)
create-females population
(set color red
set dom-value 8.0)
ask turtles (set heading random 360
set shape "arrow"
setxy ((random (30 + 0.0)) - (30 / 2)) ((random (30 + 0.0)) - (30 / 2)))
end
;;;;;;;;;;;;; vision ;;;;;;;;;;;;;;
to-report subtract-headings (h1 h2)
ifelse abs (h1 - h2) <= 180
( report h1 - h2 )
( ifelse h1 > h2
( report h1 - h2 - 360 )
( report h1 - h2 + 360 ) )
end
;;;;;;;;;;;;; reports vision variables ;;;;;;;;;;;;;;
to-report away ( agent )
report ( 180 + towards agent )
end
to-report seen-by-myself? ( agent )
report (abs (subtract-headings ((towards agent) of myself) ((heading) of myself))) <= (((vision-angle) of myself) / 2)
end
to-report other-turtles
report turtles with (self != myself)
end
to-report visible-turtles (ViewSight angle)
report other-turtles in-radius ViewSight with (seen-by-myself? self)
end
to-report visible-females (ViewSight angle)
report other-turtles in-radius ViewSight with (seen-by-myself? self and breed = females)
end
to-report nearest (agentset)
report min-one-of agentset (distance myself) ;;find nearest agent in a group
end
;;;;;;;;;;;;; interaction procedure ;;;;;;;;;;;;;;
to interact
let winner 0
let loser 0
let mentalV 0
let chaseD 0
let fleeD 0
let yyy 0
set chaseD 1 ;; winner's chasing distance
set fleeD 2 ;; loser's fleeing distance

```

```

set opponent nearest visible-turtles PerSpace vision-angle
set heading towards opponent
if distance opponent <= PerSpace
  (if (breed = males)(set male male + 1)
  if (breed = females) (set female female + 1)
  set mentalV ((dom-value) of self)/((dom-value) of self + (dom-value) of opponent)
  ifelse (mentalV > random-float 1.00)
    (set winner self
    set loser opponent)
  (set winner opponent
  set loser self)
  if (winner = self)( fight ))
end
;;;;;;;;;;;;;;;;;;;;;;;; fighting ;;;;;;;;;;;;;;;;;;;;;;;;;;
to fight
  let winner 0
  let loser 0
  let relativeV 0
  let chaseD 0
  let fleeD 0
  let yyy 0
  if (breed = males) and ((breed) of opponent = females) (set aggmale aggmale + 1)
  if (breed = females) and ((breed) of opponent = males) ( set aggfemale aggfemale + 1)
  set relativeV ((dom-value) of self)/((dom-value) of self + (dom-value) of opponent)
  ifelse (relativeV > random-float 1.00)
    (set w 1
    set winner self
    set loser opponent)
    (set w 0
    set winner opponent
    set loser self)
  if breed = males (set StepDom 1 * intensity-of-aggression
  set male male + 1)
  if breed = females (set StepDom 0.8 * intensity-of-aggression
  set female female + 1)
  set (dom-value) of self ((dom-value) of self)+(w - relativeV) * StepDom
  set (dom-value) of opponent ((dom-value) of opponent)-(w - relativeV) * StepDom
  set (dom-value) of loser max (list min-dom (dom-value) of loser ) ;;ensure dominance values of agents are above
  0.01
  ask winner (set heading towards loser fd chaseD) ;; the winner moves one unit towards its opponent, loser makes
  a 180 degree turn
  ask loser (set heading away winner + random 45 fd fleeD) ;; and flees away two until under a small random
  angle 45 degree
  ask turtles in-radius NearView (if (myself != winner) (if (seen-by-myself? winner)
  (set waitcount waitcount - 1)))
end
;;;;;;;;;;;;;;;;;;;;;;;; grouping procedure ;;;;;;;;;;;;;;;;;;;;;;;;;;
to group
  ifelse any? visible-turtles NearView vision-angle
    (ifelse attraction? (
    ifelse (breed = males)
      (if (any? visible-females NearView vision-angle)
      (set heading towards nearest visible-females NearView vision-angle fd 1))
      (fd 1))
      (fd 1))
    (ifelse any? visible-turtles MaxView vision-angle

```

```

(set heading towards nearest visible-turtles MaxView vision-angle
fd 1)
(ifelse (random-float 1.0) > 0.5 (rt search-angle / 2 lt search-angle fd 1)
(lt search-angle / 2 rt search-angle fd 1)))
end
;;;;;;;;;;;;; integration procedure ;;;;;;;;;;;;;;
to integrate
ifelse any? visible-turtles PerSpace vision-angle
(interact)
(group)
end
;;;;;;;;;;;;; go procedure ;;;;;;;;;;;;;;
to go
ask turtles (
ifelse (waitcount <= 0)
(integrate
set waitcount random 10)
(set waitcount waitcount - 1))
set time-units time-units + 1
if remainder time-units 160 = 0
(do-plot1 do-plot2)
if time-units >= 32000
(report-centrality) if time-units = 42800
(file-close
stop)
;;;;;;;;;;;;; report centrality ;;;;;;;;;;;;;;
to report-centrality
let vectors 0
ask turtles (
set vectors (towards myself) of other-turtles
hatch 1 ( measure-vectors vectors report-distance die))
end
to measure-vectors (vectors)
if (vectors != ())
(set heading (first vectors) ;go 1 in direction of first element in list
forward 1
measure-vectors (butfirst vectors) ;then do this to the rest of the elements)
end
to report-distance
ask myself (file-type precision distance myself 3 file-type ", ")
end
;;;;;;;;;;;;; plots ;;;;;;;;;;;;;;
to do-plot1
set-current-plot "Males/Females"
set-current-plot-pen "males"
plot report-boys
set-current-plot-pen "females"
plot report-girls
end
to-report differentiation
let mean-dom-value 0
let sd-dom-value 0
set mean-dom-value mean (dom-value) of turtles
set sd-dom-value standard-deviation (dom-value) of turtles
report precision (sd-dom-value / mean-dom-value) 3
end

```

```

to-report report-boys
report precision mean ( dom-value ) of males 3
end
to-report report-girls
report precision mean ( dom-value ) of females 3
end
to-report girls-beating-boys
let total-beat-boys 0
let girl-power 0
set total-beat-boys 0
foreach ((self) of females) (
set girl-power (dom-value) of ?1
foreach ((self) of males) (
if ( (dom-value) of ?1 < girl-power)
( set total-beat-boys total-beat-boys + 1)
))
report total-beat-boys
end
to do-plot2
set-current-plot "differentiation of dominance"
plot differentiation
end

```

## Dominance inheritance model

```

;This research funded by The Engineering and Physical Sciences Research Council (EPSRC),
;Grant GR/S79299/01 (AIBACS),
;“The Impact of Durative Variable state on the Design and Control of Action Selection”.

```

```

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
globals
(time-units
vision-angle
offspring
eaten
starved
highage)
;;;;;;;;;;;;;;;;; breeds ;;;;;;;;;;;;;;;;;
breed (monkeys)
;;;;;;;;;;;;;;;;; monkey variablen ;;;;;;;;;;;;;;;;;
turtles-own
(energy
dom-value
diff
distlist
mindist
opponent
age)
;;;;;;;;;;;;;;;;; setup-procedure ;;;;;;;;;;;;;;;;;
to setup
ca
setup-globals
setup-patches
setup-turtles

```



```

do-plots
end
;;;;;;;;;;;;; creates background ;;;;;;;;;;;;;;
to setup-patches
ask patches
(ifelse random-float 100 < density
(set pcolor green)
(set pcolor yellow))
if clustered?
(ask patches
(ifelse pcolor = green
(ask neighbors (set pcolor green))
(ask neighbors (set pcolor yellow))))
end
;;;;;;;;;;;;; global - variables ;;;;;;;;;;;;;;
to setup-globals
set vision-angle 170
end
;;;;;;;;;;;;; creates male and female monkeys ;;;;;;;;;;;;;;
to setup-turtles
create-monkeys Population
(set color red
set energy 40
set heading random 360
set shape "circle"
set dom-value (random-float 1) + 1
setxy (0 - random 20)(0 - random 20)
set age 0)
;;;;;;;;;;;;; reporters ;;;;;;;;;;;;;;
to-report meandom
ifelse count monkeys > 0
(report mean (dom-value) of monkeys)
(report 0)
end
to-report visible-turtles (ViewSight angle)
report other turtles in-cone ViewSight angle
end
to-report visible-monkeys (ViewSight angle)
report other monkeys in-cone ViewSight angle
end
to-report nearest (agentset)
report min-one-of agentset (distance myself)
end
to-report nearest-distance (agentset)
if nearest agentset with (self != myself) = nobody (report 0)
report distance nearest (agentset with (self != myself))
end
to-report local-cm
if breed = monkeys
(let local-monkeys turtles with (breed = (breed) of myself) in-radius MaxView
report (list (sum (xcor) of local-monkeys / (count local-monkeys)) (sum (ycor) of local-monkeys / (count local-monkeys))))
end
to-report distance-groupcenter
report distancexy (first local-cm) (last local-cm)
end

```

```

;;;;;;;;;;;;; Feeding ;;;;;;;;;;;;;;
to-report find-closest-food
report min-one-of (patches in-radius 20 with (pcolor = green)) (distance myself)
end
to move-to-monkey-food
ask (turtle-set monkeys)
(if energy < 20 (face find-closest-food fd 1))
end
to eat-monkey-food
ask (turtle-set monkeys)
(if pcolor = green
(set pcolor brown
set energy (energy + food-value)))
end
to regrow-food
ask patches (
if (time-units mod 5 = 0) and (random 100 < regrowth-rate) and (pcolor = brown)
(set pcolor green))
end
;;;;;;;;;;;;; move-turtles Egal ;;;;;;;;;;;;;;
to move-turtles
let foe 0
ask turtles(
if breed = monkeys
(let close-monkeys visible-monkeys NearView vision-angle
ifelse any? close-monkeys
(ifelse distance nearest close-monkeys < (Perspace) ;* dom-value)
(set foe nearest close-monkeys
ifelse ((dom-value) of self > (dom-value) of foe)
(chase-foe self foe)
(chase-foe foe self))
(fd 1))
(let distant-monkeys visible-monkeys MaxView vision-angle
ifelse any? distant-monkeys
(face nearest distant-monkeys
while (distance nearest distant-monkeys > 3)(face nearest distant-monkeys fd 1))
(let group-center local-cm
facexy (first local-cm) (last local-cm)
fd 1))
set energy energy - energy-cost))
end
to chase-foe (chaser chasee)
ask chaser (face chasee)
ask chasee
(face chaser
rt 158 + random 45
fd fleeingDist)
ask chaser (fd 1)
end
;;;;;;;;;;;;; reproduce ;;;;;;;;;;;;;;
to reproduce-monkeys
ask monkeys
(if energy > 1.5 * reproduction-cost
(set energy energy - reproduction-cost
hatch 1 ( set energy 40
set dom-value (((dom-value) of myself + random-float 0.2) - 0.1)

```

```

set age 0
rt random 360
fd 1
set offspring offspring + 1)))
end
;;;;;;;;;;;;; death ;;;;;;;;;;;;;;
to check-starved
ask (turtle-set monkeys)
(if energy <= 0
(set starved starved + 1
die))
end
to check-aged
ask (turtle-set monkeys)
(set age age + 1
if monkeys-age? and age > monkey-life-span
(set highage highage + 1
die))
end
;;;;;;;;;;;;; statistical predation ;;;;;;;;;;;;;;
to kill
let numprey 0
let preylist 0
ask turtles (set preydist distance-groupcenter)
set numprey ifelse-value (PredationRate = 0) (0) (int ((count turtles) * (.01 * PredationRate)))
set preylist sublist ( sort-by ( (preydist) of ?1 > (preydist) of ?2 ) turtles ) 0 numprey
foreach preylist (ask ?
(set eaten eaten + 1
die))
end
;;;;;;;;;;;;; go procedure ;;;;;;;;;;;;;;
to go
move-turtles
move-to-monkey-food
eat-monkey-food
reproduce-monkeys
resize-by-dominance
check-starved
check-aged
if time-units mod hunting-time = 0 and time-units != 0
(kill)
regrow-food
do-plots
set time-units time-units + 1
tick
end
;;;;;;;;;;;;; resize ;;;;;;;;;;;;;;
to resize-by-dominance
ask (turtle-set monkeys) (set size 1 + dom-value * 3)
end
;;;;;;;;;;;;; plots ;;;;;;;;;;;;;;
to do-plots
set-current-plot "Agents"
set-current-plot-pen "Monkeys"
if (count monkeys >= 1)
(carefully ( plot count monkeys) (plot 0))

```

```

set-current-plot-pen "Pred"
if (count predators >= 1)
(carefully ( plot count predators ) (plot 0))
set-current-plot "Mean Dominance Value"
set-current-plot-pen "Monkeys"
if (count monkeys > 0)
(plot meandom)

```

## Dominance Inheritance Model

```

population 20
PredationRate 15
hunting-time 10
reproduction-cost 44
energy-cost 4
food-value 6
Perspace 6
Nearview 16
MaxView 40
FleeingDist 1 or 2
monkey-life-span 100
regrowth-rate 45
vision-radius 50

```

## MSI model

```

; This research funded by The Engineering and Physical Sciences Research Council (EPSRC),
; Grant GR/S79299/01 (AIBACS),
; "The Impact of Durative Variable state on the Design and Control of Action
Selection".
;;;;;;;;;;;;;;;;; globale Variablen ;;;;;;;;;;;;;;;;;
globals (
time-units ;monitor to show the number of goes
vision-angle ;in what direction the turtle can see
search-angle ;where the turtle searches for other agents
grooming-radius
Desp-starved
Egal-starved
Desp-eaten
Egal-eaten
Desp-offspring

```

```

Egal-offspring)
;;;;;;;;;;;;; breeds ;;;;;;;;;;;;;;
breed (monkeysdesp)
breed (monkeysegal)
;;;;;;;;;;;;; monkey variablen ;;;;;;;;;;;;;;
turtles-own (
energy
itchyness
dom-value
diff
distlist
preydist
mindist
opponent)
;;;;;;;;;;;;; setup-procedure ;;;;;;;;;;;;;;
to setup
ca
setup-globals
setup-patches
setup-turtles
do-plots
end
;;;;;;;;;;;;; creates background ;;;;;;;;;;;;;;
to setup-patches
ask patches
(ifelse random-float 100 < density
(set pcolor green)
(set pcolor yellow))
if clustered?
(ask patches
(ifelse pcolor = green
(ask neighbors ( set pcolor green))
(ask neighbors ( set pcolor yellow))))
end
;;;;;;;;;;;;; global - variables ;;;;;;;;;;;;;;
to setup-globals
set vision-angle 170
set search-angle 90
set grooming-radius 20
end
;;;;;;;;;;;;; creates male and female monkeys ;;;;;;;;;;;;;;
to setup-turtles
create-monkeysdesp Population
(set color red
set energy 40
set itchyness random-float 60
set heading random 360
set shape "circle"
set dom-value random-float 1
setxy ((35) - random (20)) ((35) - random (20)))
create-monkeysegal Population
(set color blue
set energy 40
set itchyness random-float 60
set heading random 360
set shape "circle"

```

```

set dom-value random-float 1
setxy ((-35) - random (20)) ((-35) - random (20))
end
;;;;;;;;;;;;;;;; reports vision variables ;;;;;;;;;
to-report away (agent)
report (180 + towards agent)
end
to-report visible-turtles (ViewSight angle)
report other turtles in-cone ViewSight angle
end
to-report visible-monkeysdesp (ViewSight angle)
report other monkeysdesp in-cone ViewSight angle
end
to-report visible-monkeysegal (ViewSight angle)
report other monkeysegal in-cone ViewSight angle
end
to-report nearest (agentset)
report min-one-of agentset (distance myself)
end
to-report nearest-distance (agentset)
if nearest agentset with (self != myself) = nobody (report 0)
report distance nearest (agentset with (self != myself))
end
;;;;;;;;;;;;;;;; Feeding ;;;;;;;;;
to-report find-closest-food
report min-one-of (patches in-radius 20 with (pcolor = green)) (distance myself)
end
to move-to-food
ask turtles
(if energy < 20 ( face find-closest-food fd 1))
end
to eat-food
ask turtles
(if pcolor = green
(set pcolor brown
set energy (energy + food-value)))
end
to regrow-food
ask patches (
if (time-units mod 5 = 0) and (random 100 < regrowth-rate) and (pcolor = brown)
(set pcolor green))
end
;;;;;;;;;;;;;;;; move-turtles Egal ;;;;;;;;;
to move-turtlesegal
let foe 0
ask turtles(
if breed = monkeysegal (
let close-monkeys visible-monkeysegal EgalNearView vision-angle
ifelse any? close-monkeys
(ifelse distance nearest close-monkeys < EgalPerspace
(set foe nearest close-monkeys
ifelse ((dom-value) of self > (dom-value) of foe)
(chase-foe self foe)
(chase-foe foe self))
(fd 1))
(let distant-monkeys visible-monkeysegal EgalMaxView vision-angle

```

```

ifelse any? distant-monkeys (
  face nearest distant-monkeys
  while (distance nearest distant-monkeys > 3) (fd 1))
(facexy (first local-cm) (last local-cm)
  fd 1))
set energy energy - energy-cost))
end
to move-turtlesdesp
let foe 0
ask turtles(
  if breed = monkeysdesp
  (let close-monkeys visible-monkeysdesp DespNearView vision-angle
  ifelse any? close-monkeys
  (ifelse distance nearest close-monkeys < DespPerspace
  (set foe nearest close-monkeys
  ifelse ((dom-value) of self > (dom-value) of foe)
  (chase-foe self foe)
  (chase-foe foe self))
  (fd 1))
  (let distant-monkeys visible-monkeysdesp DespMaxView vision-angle
  ifelse any? distant-monkeys
  (face nearest distant-monkeys
  while (distance nearest distant-monkeys > 3)
  (fd 1))
  (let group-center local-cm
  facexy (first group-center) (last group-center)
  fd 1))
  set energy energy - energy-cost
  set itchyiness itchyiness + 1))
end
to chase-foe (chaser chasee)
ask chaser (face chasee)
ask chasee (
  face chaser
  rt 158 + random 45
  fd 2)
ask chaser (fd 1)
end
;;;;;;;;;;;;; calculate the center of mass ;;;;;;;;;;;;;;
to-report local-cm
let local-monkeys turtles with (breed = (breed) of myself) in-radius vision-radius
report (list (sum (xcor) of local-monkeys / (count local-monkeys)) (sum (ycor)
  of local-monkeys / (count local-monkeys)))
end
;;;;;;;;;;;;; reproduce ;;;;;;;;;;;;;;
to reproduce
ask turtles(
  if energy > 60 (
  set energy energy - reproduction-cost
  hatch 1 (set energy 40
  set dom-value ((dom-value) of myself) + random-normal 0.0 0.2
  rt random 360
  fd 1
  ifelse breed = monkeysdesp
  (set Desp-offspring Desp-offspring + 1)
  (set Egal-offspring Egal-offspring + 1))))

```

```

end
;;;;;;;;;;;;;;;;; death ;;;;;;;;;;;;;;;;;;
to check-death
ask turtles (
if energy <= 0 (
ifelse breed = monkeysdesp
(set Desp-starved desp-starved + 1)
(set Egal-starved egal-starved + 1)
die))
end
;;;;;;;;;;;;;;;;; predation ;;;;;;;;;;;;;;;;;;
to kill
let numprey 0
let preylst 0
ask turtles (set preydist nearest-distance turtles)
set numprey ifelse-value (PredationRate = 0) (0) (int ((count turtles) * (.01 * PredationRate)))
set preylst sublist (sort-by ((preydist) of ?1 > (preydist) of ?2) turtles) 0 numprey
foreach preylst (ask ?
(ifelse breed = monkeysdesp
(set Desp-eaten Desp-eaten + 1)
(set Egal-eaten Egal-eaten + 1)
die))
end
;;;;;;;;;;;;;;;;; go procedure ;;;;;;;;;;;;;;;;;;
to go
move-turtlesdesp
move-turtlesegal
move-to-food
eat-food
reproduce
normalize-dom-value monkeysegal
normalize-dom-value monkeysdesp
resize-by-dominance
check-death
if time-units mod hunting-time = 0 and time-units != 0
(kill)
regrow-food
do-plots
set time-units time-units + 1
tick
end
;;;;;;;;;;;;;;;;; normalize ;;;;;;;;;;;;;;;;;;
to normalize-dom-value (monkeyset)
if (not any? monkeyset) (stop)
let maxd max (dom-value) of monkeyset
let mind min (dom-value) of monkeyset
let diffd maxd - mind
if (diffd != 0)
(ask monkeyset (set dom-value (dom-value - mind) / diffd))
end
;;;;;;;;;;;;;;;;; resize ;;;;;;;;;;;;;;;;;;
to resize-by-dominance
ask turtles (set size 1 + dom-value * 5)
end
;;;;;;;;;;;;;;;;; plots ;;;;;;;;;;;;;;;;;;
to do-plots

```



```

set-current-plot "Agents"
set-current-plot-pen "Desp"
carefully ( plot count monkeysdesp ) (plot 0)
set-current-plot-pen "Egal"
carefully (plot count monkeysegal) (plot 0)
set-current-plot "Dominance"
set-current-plot-pen "Desp"
if (count monkeysdesp > 2)
( plot mean (dom-value) of monkeysdesp )
set-current-plot-pen "Egal"
if (count monkeysegal > 2)
(plot mean (dom-value) of monkeysegal )
set-current-plot "Egalitarian Dominance"
set-histogram-num-bars 10
histogram (dom-value) of monkeysegal
set-current-plot "Despotic Dominance"
set-histogram-num-bars 10
histogram (dom-value) of monkeysdesp
end

```

## Parameter settings for MSI Models

```

clustered? on or off
population 20
PredationRate 12.5
hunting-time 10
reproduction-cost 32
energy-cost 4
food-value 6
DespPerspace 6
DespNearview 15
DespMaxView 20
EgalPerspace 3
EgalNearview 15
EgalMaxView 40
density 80 or 100
clustered on or off
vision-radius 40
regrowth-rate 40
food-value 6

```

## Extensions of dominance inheritance model

```
;This research funded by The Engineering and Physical Sciences Research Council (EPSRC),
;Grant GR/S79299/01 (AIBACS),
;"The Impact of Durative Variable state on the Design and Control of Action Selection".
;;;;;;;;;;;;;;;;; globale Variablen ;;;;;;;;;;;;;;;;;;
globals(
time-units ;monitor to show the number of goes
vision-angle ;in what direction the turtle can see
search-angle ;where the turtle searches for other agents
offspring-female
offspring-male
offspring-no-sex
starved-female
starved-male
eaten-female
eaten-male
highage)
;;;;;;;;;;;;;;;;; breeds ;;;;;;;;;;;;;;;;;;
breed (monkeys)
breed (females)
breed (males)
;;;;;;;;;;;;;;;;; monkey variablen ;;;;;;;;;;;;;;;;;;
turtles-own
(energy
dom-value ;hierarchy variablen
fitness ; in the males, the same as fitness, in females, hidden by mother's rank
diff ;the actual vision angle between two agents
distlist
preydist
mindist
opponent
age)
;;;;;;;;;;;;;;;;; setup-procedure ;;;;;;;;;;;;;;;;;;
to setup
ca
setup-globals
setup-patches
setup-turtles
do-plots
end
;;;;;;;;;;;;;;;;; creates environment ;;;;;;;;;;;;;;;;;;
to setup-patches
ask patches
(ifelse random-float 100 < density
(set pcolor green)
(set pcolor yellow))
if clustered?
(ask patches
(ifelse pcolor = green
(ask neighbors (set pcolor green))
(ask neighbors (set pcolor yellow))))
end
;;;;;;;;;;;;;;;;; global - variables ;;;;;;;;;;;;;;;;;;
to setup-globals
```

```

set vision-angle 170
set search-angle 90
end
;;;;;;;;;;;;; creates male and female monkeys ;;;;;;;;;;;;;;
to setup-turtles
create-monkeys Population
(ifelse (random-float 1 < .5)
(set breed females
set color red
set energy 40
set heading random 360
set shape "circle"
set dom-value random-normal 5 0.3
set fitness dom-value
set age 0
setxy ((0) - random (20)) ((0) - random (20)))
(set breed males
set color blue
set energy 40
set heading random 360
set shape "circle"
set dom-value random-normal 5 0.3
set fitness dom-value
set age 0
setxy ((0) - random (20)) ((0) - random (20))))
end
;;;;;;;;;;;;; reports vision variables ;;;;;;;;;;;;;;
to-report male-dominance
ifelse (count males > 1)
(report mean (dom-value) of males)
(report 0)
end
to-report pop-dominance
ifelse (count turtles > 1)
(report mean (dom-value) of turtles)
(report 0)
end
to-report visible-turtles (ViewSight angle)
report other turtles in-cone ViewSight angle
end
to-report maleCV-fit
report sqrt (variance (fitness) of males)
end
to-report femaleCV-fit
report sqrt (variance (fitness) of females)
end
to-report maleCV-dom
report sqrt (variance (dom-value) of males)
end
to-report femaleCV-dom
report sqrt (variance (dom-value) of females)
end
to-report nearest (agentset)
report min-one-of agentset (distance myself)
end
to-report nearest-distance (agentset)

```

```

if nearest agentset with (self != myself) = nobody (report 0)
report distance nearest (agentset with (self != myself))
end
;;;;;;;;;;;;; calculate the center of mass ;;;;;;;;;;;;;;
to-report local-cm
let local-monkeys turtles in-radius vision-radius
report (list (sum (xcor) of local-monkeys / (count local-monkeys)) (sum (ycor) of local-monkeys / (count local-monkeys)))
end
to-report distance-groupcenter
report distancexy (first local-cm) (last local-cm)
end
;;;;;;;;;;;;; Feeding ;;;;;;;;;;;;;;
to-report closest-food
report min-one-of (patches in-radius 20 with (pcolor = green)) (distance myself)
end
to move-to-food
ask turtles
(if energy < 20 (face closest-food fd 1))
end
to eat-food
ask turtles
(if pcolor = green
(set pcolor brown
set energy (energy + food-value)))
end
to regrow-food
ask patches (
if (time-units mod 5 = 0) and (random 100 < regrowth-rate) and (pcolor = brown)
(set pcolor green))
end
;;;;;;;;;;;;; move-turtles Egal ;;;;;;;;;;;;;;
to move-turtles
let foe 0
ask turtles (
let close-turtles visible-turtles NearView vision-angle ; get all monkeys that are visible within NearView
ifelse any? close-turtles
(ifelse distance nearest close-turtles < Perspace
(set foe nearest close-turtles
ifelse ((fitness) of self > (fitness) of foe)
(chase-foe self foe)
(chase-foe foe self))
(fd 1))
(let distant-turtles visible-turtles MaxView vision-angle
ifelse any? distant-turtles
(face nearest distant-turtles
while (distance nearest distant-turtles > 3) (fd 1))
(facexy (first local-cm) (last local-cm)
fd 1))
set energy energy - energy-cost)
end
to chase-foe (chaser chasee)
ask chasee
(face chaser
rt 180 + random 25
fd 3)

```

```

ask chaser (
face chasee
fd 1)
end
;;;;;;;;;;;;;;;;; reproduce ;;;;;;;;;;;;;;;;;;
to reproduce
ask turtles (
if energy > 60 (
set energy energy - reproduction-cost
hatch 1 ( set energy reproduction-cost
set dom-value ((dom-value) of myself) + random-normal 0.0 0.1
set fitness ((fitness) of myself) + random-normal 0.0 0.1
set offspring-no-sex offspring-no-sex + 1
set age 0
rt random 360
fd 1)))
end
to reproduce-sexually
let partner nobody
ask turtles (
if ((breed = females) and (energy > 60))
(ifelse (fem-mate-choice = true)
(set partner max-one-of (turtles in-radius mate-choice-range with ((breed = males) and (energy > 30)))
(dom-value))
(set partner min-one-of (turtles in-radius mate-choice-range with ((breed != myself) and (energy > 30)))
(distance myself))
if (partner != nobody) (
set energy energy - reproduction-cost
hatch 1 ( set energy reproduction-cost
ifelse (random-float 1 < .5)
(set breed females
set offspring-female offspring-female + 1
set color red
set age 0
rt random 360
fd 1
set fitness (((fitness) of partner + (fitness) of myself) / 2) + random-normal 0.0 0.1
set dom-value ((dom-value) of myself) + random-normal 0.0 0.01)
(set breed males
set offspring-male offspring-male + 1
set color blue
set shape "circle"
rt random 360
fd 1
set age 0
set fitness (((fitness) of partner + (fitness) of myself) / 2) + random-normal 0.0 (male-variation) ;
males should vary more than females
set dom-value fitness + random-normal 0.0 0.01)
rt random 360
fd 1))))
end
;;;;;;;;;;;;;;;;; death ;;;;;;;;;;;;;;;;;;
to check-death
ask turtles (
if energy <= 0 (
ifelse (breed = females)

```

```

(set starved-female starved-female + 1)
(set starved-male starved-male + 1)
die))
end
to check-aged
ask turtles
(set age age + 1
if age > monkey-life-span
(set highage highage + 1
die))
end
;;;;;;;;;;;;;;;;; predation ;;;;;;;;;;;;;;;;;;
to kill
let numprey 0
let preylst 0
ask turtles (set preydist distance-groupcenter)
set numprey ifelse-value (PredationRate = 0) (0) (int ((count turtles) * (.01 * PredationRate)))
set preylst sublist ( sort-by ( (preydist) of ?1 > (preydist) of ?2 ) turtles ) 0 numprey
foreach preylst (ask ? (
ifelse (breed = females)
(set eaten-female eaten-female + 1)
(set eaten-male eaten-male + 1)
die))
end
;;;;;;;;;;;;;;;;; go procedure ;;;;;;;;;;;;;;;;;;
to go
move-turtles
move-to-food
eat-food
ifelse (sex? = true) (reproduce-sexually)(reproduce)
resize-by-dominance
check-death
check-aged
if time-units mod hunting-time = 0 and time-units != 0
(kill)
regrow-food
do-plots
set time-units time-units + 1
tick
end
;;;;;;;;;;;;;;;;; resize ;;;;;;;;;;;;;;;;;;
to resize-by-dominance
ask turtles ( set size 1 + dom-value * 1.5 )
end
;;;;;;;;;;;;;;;;; plots ;;;;;;;;;;;;;;;;;;
to do-plots
set-current-plot "Population Size"
set-current-plot-pen "Pop"
if (count turtles >= 1)
(carefully ( plot count turtles ) ( plot 0 ))
set-current-plot "Dominance"
set-current-plot-pen "Fem"
if (count females > 2)
(plot mean (dom-value) of females)
set-current-plot-pen "Males"
if (count males > 2)

```

```

(plot mean (dom-value) of males)
set-current-plot-pen "Pop"
if (count turtles > 2)
  (plot mean (dom-value) of turtles)
  set-current-plot "Fitness"
  set-current-plot-pen "Fem"
  if (count females > 2)
    (plot mean (fitness) of females)
    set-current-plot-pen "Males"
  if (count males > 2)
    (plot mean (fitness) of males)
    set-current-plot "Dominance Distr. Males"
  set-histogram-num-bars 20
  histogram (dom-value) of males
  set-current-plot "Dominance Distr. Females"
  set-histogram-num-bars 20
  histogram (dom-value) of females
  set-current-plot "Standard deviation of Dominance"
  set-current-plot-pen "Fem"
; if (count turtles > 2)
  carefully (plot femaleCV-dom) (plot 0)
  set-current-plot-pen "Male"
; if (count females > 2)
  carefully (plot maleCV-dom) (plot 0)
  set-current-plot "standard deviation of Fitness"
  set-current-plot-pen "Fem"
; if (count turtles > 2)
  carefully (plot femaleCV-fit) (plot 0)
  set-current-plot-pen "Male"
; if (count females > 2)
  carefully (plot maleCV-fit) (plot 0)
end

```

## Parameter settings for the extensions of the dominance inheritance model

```

sex? on or off
population 20
PredationRate 12.5
hunting-time 10
reproduction-cost 32
regrowth-rate 33
energy-cost 4
food-value 6
Perspace 6
Nearview 16

```

MaxView 40  
density 100  
mate-choice-range 16  
monkey-life-span 150  
vision-radius 30  
clustered? off  
female-mate-choice on off